SOME ASPECTS OF THE ECOLOGY OF THE SMALL, WINTER-ACTIVE MAMMALS OF A FIELD AND ADJACENT WOODS IN ITASCA STATE PARK, MINNESOTA

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF

THE UNIVERSITY OF MINNESOTA

BY

elcton
ERNEST B. BROWN, III

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR

THE DEGREE OF DOCTOR OF PHILOSOPHY

DEGREE GRANTED

MARCH 1971

TABLE OF CONTENTS

Table of Contents Continued

Ernest Benton Brown III
572

Some Aspects of the Ecology of the Small, Winter-Active Mammals of a Field and Adjacent Woods in Itasca State Park, Minnesota

The purpose of this study was three-fold. First, to determine if there are seasonal changes in distribution of small winter-active mammals across a sharp wood-meadow transition; second, to gather field growth data on these animals: and third, to evaluate and develop a winter live-trapping technique.

A live-trapping study was conducted in an old field and adjacent stands of planted jack pine (Pinus banksiana), planted red pine (Pinus resinosa), young aspen (Populus tremuloides), and mature aspen in north-central Minnesota from July 1965 through March 1968. Live-traps were set in a grid pattern with 35 feet between traps. The traps were maintained in wooden chimneys, which made it possible to trap below the snow cover in the winter without disturbing the snow cover. Distribution, and weight and measurement records were maintained for all winter-active mammals trapped.

Meadow mice (Microtus pennsylvanicus) were found in the meadow, young aspen, and red pine in the snow-free months, but were most heavily concentrated in the meadow. In the winter meadow mice were found only in the meadow and primarily in the part of the meadow where brome grass (Bromus inermis) is dominant. Red-backed voles (Clethrionomys gapperi) were found only in the mature and young aspen habitats during both winter and snow-free seasons. This species was equally distributed between these habitats during the winter but was more concentrated in the mature aspen during the snow-free season. There was no indication of individual movement between seasons in either of these species. Deer mice (Peromyscus sp.) were concentrated in the mature aspen during the snow-free season and there was only one winter capture of this species. Short-tailed shrews (Blarina brevicauda) were distributed equally across all habitats during the snow-free season and were distributed equally across all but the avoided Poa-Phleum-Carex portion of the meadow during the winter. The possible effect on distribution of interactions between all these species is discussed.

A measurement of the reliability of weights and measurements made on living small mammals is given and indicates that linear measurements are a great deal more reliable than weight measurements.

M. pennsylvanicus born by early May reached their maximum size by late July and underwent a sharp loss in weight starting in early August. Microtus born after early or mid-May experienced a seasonal stoppage of growth by late August to mid-September. There was then no growth until sometime between mid-March and early April. B. brevicada captured in the winter were as large and heavy as the summer animals. The evidence indicated that there was no weight loss in the fall.

Acivity of M. pennsylvanicus appeared to be equal in all three periods of the day during the snow-free trapping sessions but was more heavily concentrated in the 1600-2400 period during the winter sessions. Activity of C. gapperi appeared to be equal in all three periods of the day during the winter sessions. Activity of Peromyscus sp. was restricted to the 1600-2400 period during the snow-free season. B. brevicauda were arhythmic with respect to a diel activity pattern during both the winter and snow-free seasons.

The chimney technique originally developed for live-trapping small mammals in the Alaskan taiga was easily adapted to this study in northern Minnesota.

James C Underhill
Jun 15, 1971

ACKNOWLEDGEMENTS

I wish to express my thanks to my advisor, Dr. James C. Underhill, for his suggestions and help in all phases of this study. Dr. William D. Schmid made a number of valuable suggestions concerning the statistical treatment of some of the data. My father-in-law, Mr. Howard F. Carlson, helped in the construction of the wooden chimneys used in the study and made several suggestions which materially reduced the labor involved in constructing the chimneys. A number of my fellow graduate students gave freely of their time and knowledge during the course of this study. To all of these people I am deeply indebted.

I wish to gratefully acknowledge financial support during part of the study by National Science Foundation Summer Research Stipends offered through the Itasca Biology Summer Sessions and also by an Anderson Summer Fellowship. I also wish to acknowledge the use of Itasca facilities during the course of the study, particularly the cabin used during the winter months. The traps used during the study were on loan from the Bell Museum of Natural History.

I am finally deeply indebted to my wife, Beth, for her help in typing the manuscript and for her encouragement and patience.

INTRODUCTION

It is surprising but true that there are very few studies devoted to an understanding of the winter ecology of mammals in regions with a persistent winter snow cover. Formosov's classic study (1946), in which he proposes a classification of animals on the basis of adaptation to snow cover, stirred some interest in winter ecology (primarily in Russia). He proposed that animals unable to adjust to snowy conditions be called _chionophobes_, animals which can survive in snowy regions but are not limited to them be called _chionophores_, and animals which are limited to snowy regions be called _chionophiles_.

Formosov pointed out that the three principal adaptations by mammals for life in the snow are long legs, oversize feet, and the seeking of shelter below the snow. The present study is concerned only with the small mammals which live in the subnivean space in the winter.

Dr. W. O. Pruitt, Jr., a leader in the study of the winter ecology of North American mammals, when speaking of the snow cover in the subarctic taiga, stated in 1957 that, "No other ecotone, except the hydrosphere-atmosphere interface, affords such a sharp environmental gradient...". The low thermal conductivity of snow (Elsner and Pruitt, 1959), its poor transmital of light (Pruitt, 1960), and its insulating effect against sound (Pruitt, ibid), insure a microclimate under the snow characterized by darkness, stable temperature, and silence. Pruitt (1957) showed that fluctuations in the temperature of the forest floor closely follow ambient air fluctuations until a snow depth of about 15-20 cm. is reached (the hiemal threshold). He called the time in the autumn when the temperature of the air first falls below substrate temperature the thermal overturn. After the hiemal threshold is reached the temperature beneath the snow tends to stabilize near freezing (Pruitt, 1957; Coulianos and Johnels, 1962). Johnson (1954) reported a temperature 20 degrees Fahrenheit below two feet of snow when the temperature above the snow was minus 70 degrees.

Scholander, et al (1950a, b, c) showed that fur thickness reaches a maximum useful length in the fox and that smaller mammals must have shorter and lighter fur or their movements would be hindered. Thus, although their critical temperatures are lower, the small mammals of the arctic fall within the range of tropical mammals in terms of insulation and fur thickness. For this reason and because of their very poor surface-volume ratio the small winter-active mammals are strongly dependent on the snow cover in cold weather.

Formosov (1946) and Pruitt (1959a) mention greater abundance of small mammals under thicker snow cover, presumably due to higher temperature. Coulianos and Johnels (1962) found the subnivean air space to be higher and more continuous in dense clover and timothy than in coniferous and deciduous woods. They also found that mice avoided an area of field in the winter which had been mown the previous fall. Ackerfors (1964) trapped under the snow in grassland, wood, and wood edge, and trapped the largest number of shrews in the grassland. The studies of

Coulianos and Johnels, and Ackerfors (carried out in Sweden) suggested the possibility of movement between woods and fields, due to the quality of the subnivean air space. It appeared to me that the most logical way to test this possibility would be to establish a trapping grid across a sharp wood-meadow transition in a region with deep persistent winter snow cover and live-trap the small mammals during the summer and winter seasons. By using this technique it would also be possible to gather data on the field growth of individual animals during winter as well as summer.

The greatest problem involved in carrying out such a study appeared to be how to trap the animals in the winter, beneath the snow, without disturbing the snow cover. MacKay (1962) reported that surface trapping produced no results when the snow cover was greater than 6 inches. Bergstedt (1965) in Sweden and Gunderson (1950) in Minnesota both had great difficulty in live-trapping small mammals when snow was on the ground. Pruitt (1959a) presented very preliminary results of a technique designed for live-trapping small mammals in the taiga subnivean air space. Plywood chimneys with a hinged lid and an opening on the bottom were staked in place in summer. After the snow reached a depth sufficient to support the weight of a man on snowshoes without destroying the subnivean air space traps were placed in the chimneys. Two cup hooks on each live trap were grappeled by a long metal hook to place or remove the trap from the bottom of the chimney. The technique appeared ideally suited for the present study if it would work, or could be modified to work, in northern Minnesota.

The purpose of this study was thus basically threefold. First, to determine if there are seasonal changes in distribution of small winter-active mammals across a sharp wood-meadow transition; second, to gather field growth data on these animals; and third, to evaluate and develop a winter live-trapping technique.

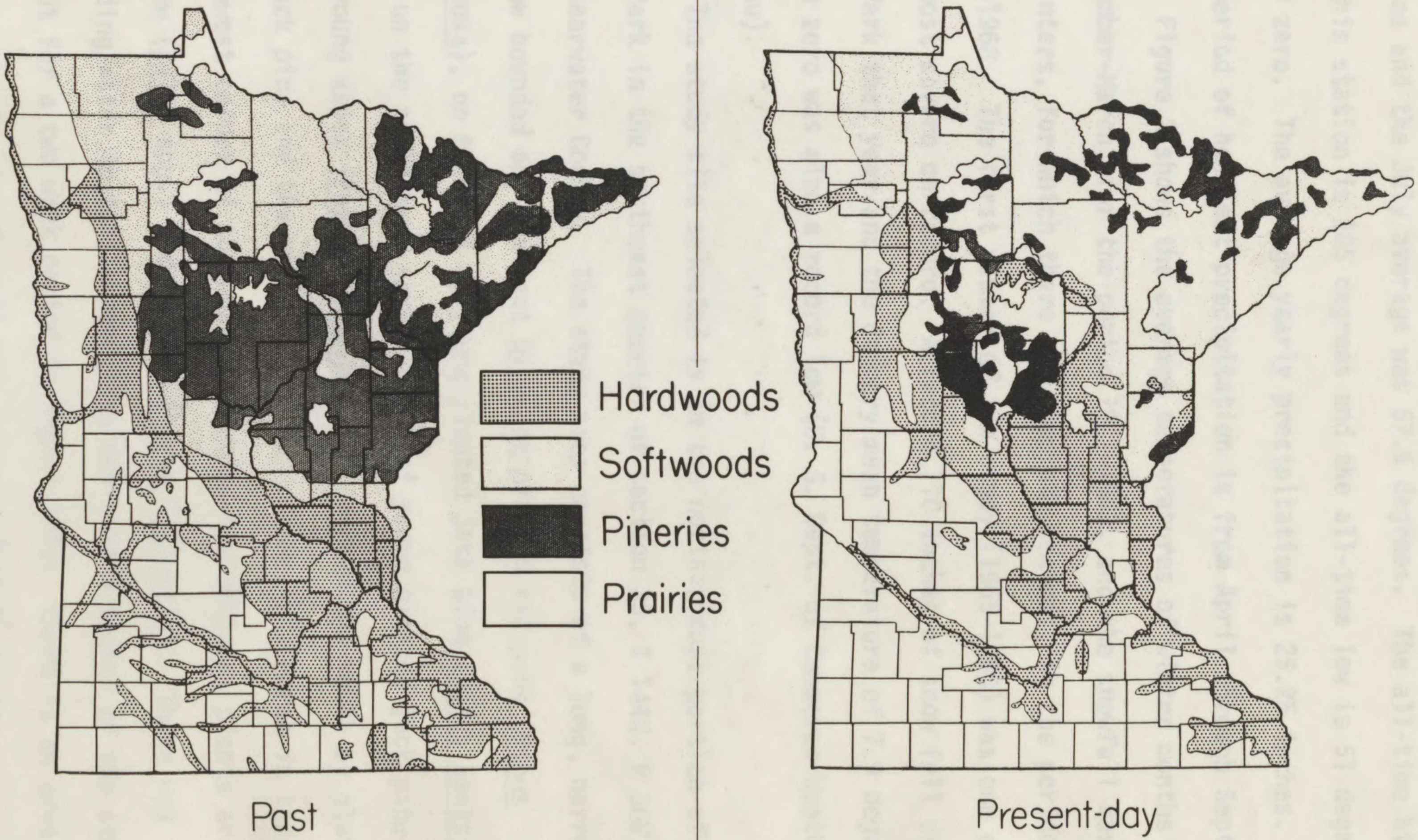
DESCRIPTION OF STUDY AREA

Itasca State Park is located in Hubbard and Clearwater Counties in north-central Minnesota. It is situated near the western edge of one of Minnesota's major vegetation types, the coniferous forest. A narrow band of deciduous forest lies to the west of the coniferous forest between the conifer forest and the tall grass prairie. Figure 1 shows the relationship of the major vegetation types in Minnesota in the mid-1800's and at the present time.

Although there are large tracts of red pine (*Pinus resinosa*), white pine (*Pinus strobus*), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) in the Park, extensive logging operations between 1901 and 1921 removed much of the best timber, and several large fires in the second half of the nineteenth century destroyed many large stands. The more recent fires and the logging operations produced large open areas which are now mature aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) stands (Dobie, 1959, pp. 119-139). There are also a few stands of mixed hardwoods in the Park consisting primarily of hard maple (*Acer saccharum*), basswood (*Tilia americana*) and bur-oak (*Quercus macrocarpa*) (Buell and Gordon, 1945).

The climate of the Itasca region is continental. Although the temperature readings taken at the Itasca Biological Station during the period 1931-1960 indicate a fairly moderate yearly average of 38.7 degrees Farenheit, the January average was 6.6

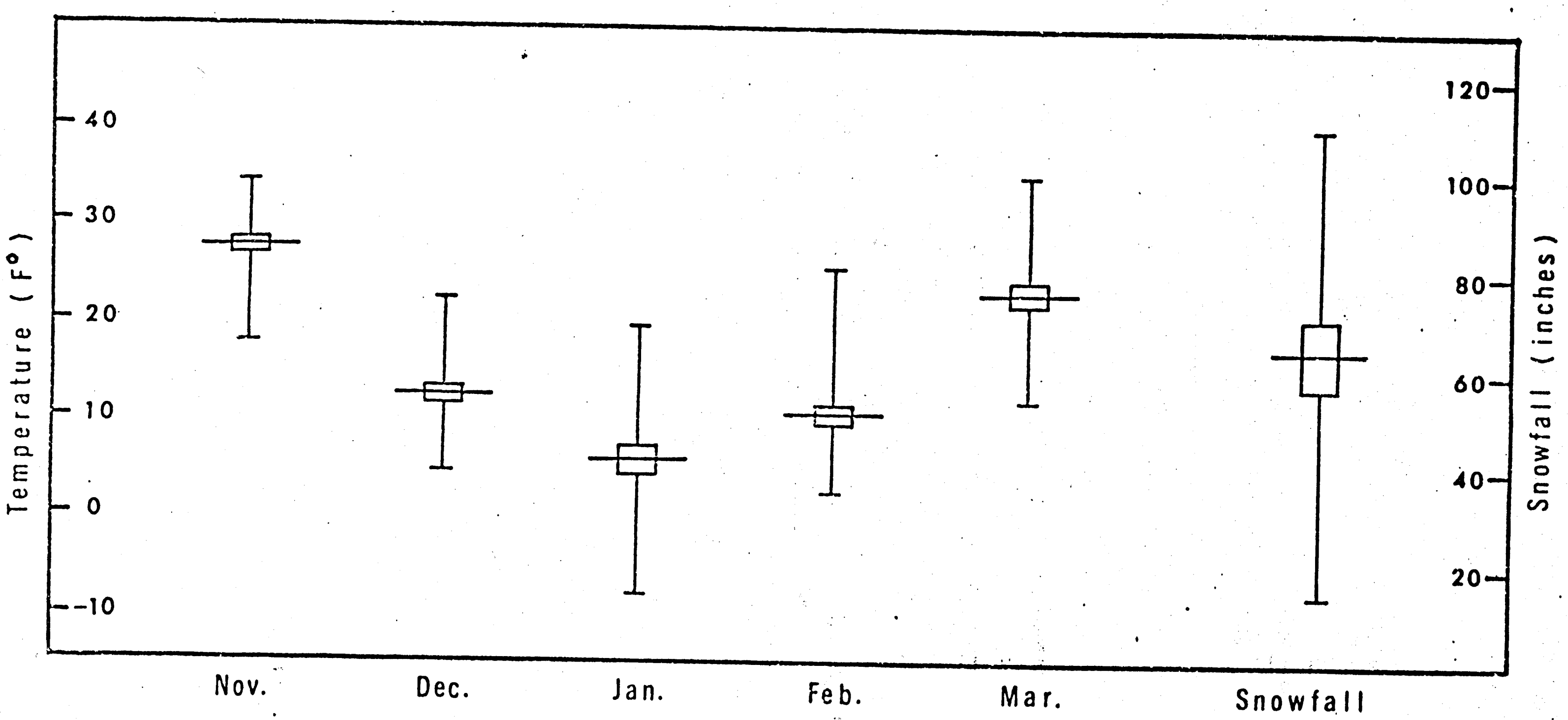
Fig. 1. Past (mid-1800's) and present distribution of major vegetation types in Minnesota.


Hardwoods
Softwoods
Pineries
Prairies
Past
Present-day

degrees and the July average was 67.6 degrees. The all-time high for this station is 105 degrees and the all-time low is 51 degrees below zero. The average yearly precipitation is 25.25 inches. The period of heaviest precipitation is from April through September. Figure 2 shows the average temperatures of winter months (November-March) for the period 1941-1968, and the snowfall during 12 winters, for which there are complete records, in the period 1950-1968. The first winter of the study (1965-1966) was one of the most severe on record. A record 110 inches of snow fell on the Park that year and the January mean temperature of 7.9 degrees below zero was also a record low (U. S. Dept. of Commerce Weather Bureau).

The study site selected is in the northernmost portion of the Park in the southeast quarter of section 35, T 144N, R 36W, in Clearwater County. The study area consists of a long, narrow meadow bounded on the east by young planted red pine (*Pinus resinosa*), on the west by young planted jack pine (*Pinus banksiana*), on the north by a narrow strip of young planted jack pine and young aspen (*Populus tremuloides*), and on the south by planted jack pine and the main park drive. There is a marsh in the southwest corner of the meadow in which the dominant plants are willow (*Salix* spp.) and cattail (*Typha latifolia*). There was standing water in this area during the entire course of the study except for a two week period in August 1965. There is an area of heavy grass cover and small bur-oaks immediately to the west of the planted jack pine. The forest surrounding the meadow and planted trees is a mature aspen stand, with the exception of an

Fig. 2. Average temperatures during winter months (1941-1968) and total winter snowfall (12 winters in the period 1950-1968). Range, mean, and plus and minus one standard error of the mean are indicated.


Temperature (F°)
40
30
20
10
0
-10
Nov.
Dec.
Jan.
Feb.
Mar.
Snowfall
120
100
80
60
40
20
Snowfall (inches)

area of large red pines at the eastern edge of the planted red pine. Because of the planted nature of the red and jack pine stands and because of other aspects of the history of the area (see below), the several wooded portions are each very homogenous and the dividing lines between various parts of the study area are very sharp (Figs. 3 and 4).

The history of the study area was worked out by interviewing several long-time residents of the area. Mr. Bert Pfeifer said that all of the study area was part of the homestead of his great-uncle, Theodore Wegmann. Mr. Wegmann and his wife, Johanna, settled in the area in 1893. Spurr (1954) said that the last of the great fires in the Park occurred in 1886 and was most severe in the northeast corner of the Park. Dobie (1959, p. 122) mentioned the same fire and said that the early settlers from 1893 to 1900 called the area at the north end of Lake Itasca "the big burn". Mr. Pfeifer said that Mr. Wegmann cleared of brush, fenced, plowed and used for crops the area now bounded by the present mature aspen forest. Large parts of the barb wire fence are still intact. The surrounding area was also used for grazing cattle. The field was plowed in 1928 for the last time. The homestead was acquired by the Park in 1945 after the death of Mr. Wegmann in 1941 and his wife, Johanna, in 1944. Mr. Miller said that the jack pines were planted in 1946 and the red pines in 1952.

The dominant plants on the meadow are bluegrass (*Poa pratensis*), quack grass (*Agropyron repens*), brome grass (*Bromus inermis*), red fescue (*Festuca rubra*), timothy (*Phleum pratense*),

Fig. 3. A diagrammatic view of the study area.

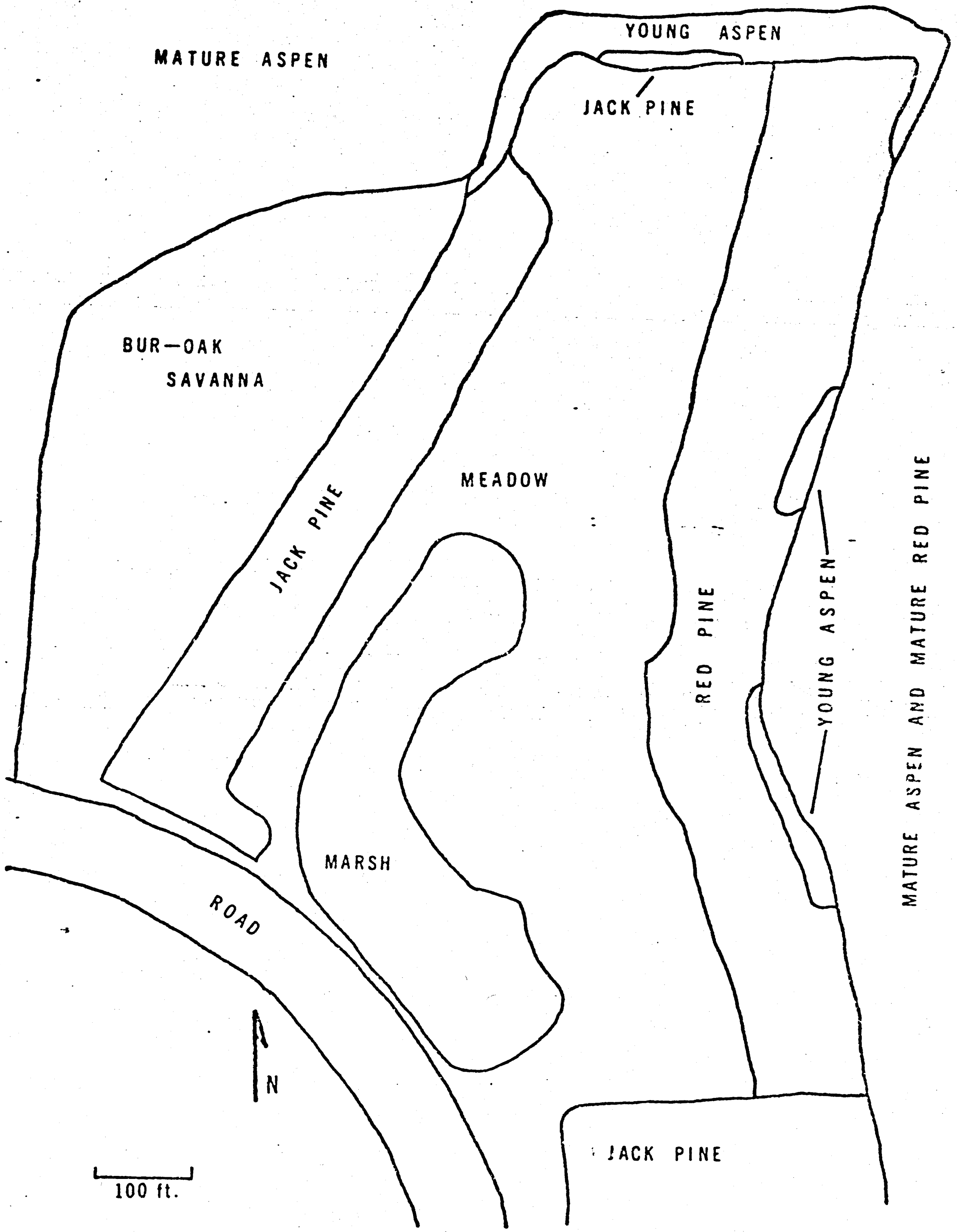

MATURE ASPEN
YOUNG ASPEN
JACK PINE
BUR—OAK
SAVANNA
MEADOW
JACK PINE
RED PINE
YOUNG ASPEN
MATURE ASPEN AND MATURE RED PINE
MARSH
ROAD
N
100 ft.
JACK PINE

Fig. 4. The study area as viewed from the road looking north.

and wild rose (*Rosa* sp.). Other plants common on the meadow are Canada anemone (*Anemone canadensis*), woolly yarrow (*Achillea millefolium*), Canada thistle (*Cirsium arvense*), Lindley's aster (*Aster ciliolatus*), sedge (*Carex rosea*), red clover (*Trifolium hybridum*). The frequency with which plant species were seen in 52 quarter meter^2 quadrats are given in Table 1. The meadow does not present a level uniform appearance and the divisions between areas dominated by different species are generally very sharp. This is particularly true in the northern portion of the meadow (Figs. 5 and 6). The litter layer on the meadow is very thick. A total of 98 measurements taken by sliding a thin plastic ruler down through the litter gave a mean litter depth of 5.3 cm. with a maximum of 9.0 cm. and a minimum of 1.5 cm.

The jack pines on the west side of the meadow were planted in straight lines and rows. The trunks of the trees are between 4 and 5 feet apart. A representative pine in this stand was 5.1 inches in diameter at breast height and 23 feet tall. The pines form a thick, almost continuous canopy and the brush and herb layers are consequently very sparse. The most common plants in these layers are dogbane (*Apocynum androsaemifolium*), wild rose (*Rosa* sp.), poison ivy (*Rhus radicans*), northern bedstraw (*Galium boreale*), and Pennsylvania sedge (*Carex pennsylvanica*). The needle litter is continuous and generally more than an inch thick (Fig. 7).

The red pines on the east side of the meadow are irregularly spaced and far enough apart so that there are open areas around most of the trees. A representative pine in this stand was 4.9

Table 1. Frequency of occurrence of species in the meadow in 52 .25 meter^2 quadrats.

Species	%
Poa pratensis	50
Agropyron repens	46
Bromus inermis	33
Rosa sp.	23
Anemone canadensis	23
Festuca rubra	19
Aster ciliolatus	17.5
Phleum pratense	17.5
Achillea millefolium	15.5
Cirsium arvense	13.5
Carex rosea	9.5
Apocynum androsaemifolium	7.5
Stachys palustris	7.5
Trifolium hybridum	7.5
Trifolium pratense	7.5
Carex atherodes	6
Thalictrum dasycarpum	6
Muhlenbergia glomerata	4
Carex pennsylvanica	2
Cirsium volgare	2
Liastris aspera	2

Cont. on next page

Table 1 Cont.

Species	%
Poa palustris	2
Scirpus cyperinus	2
Solidago canadensis	2
Spiraea alba	2
Vicia americana	2

Fig. 5. Distribution of vegetation in the meadow.

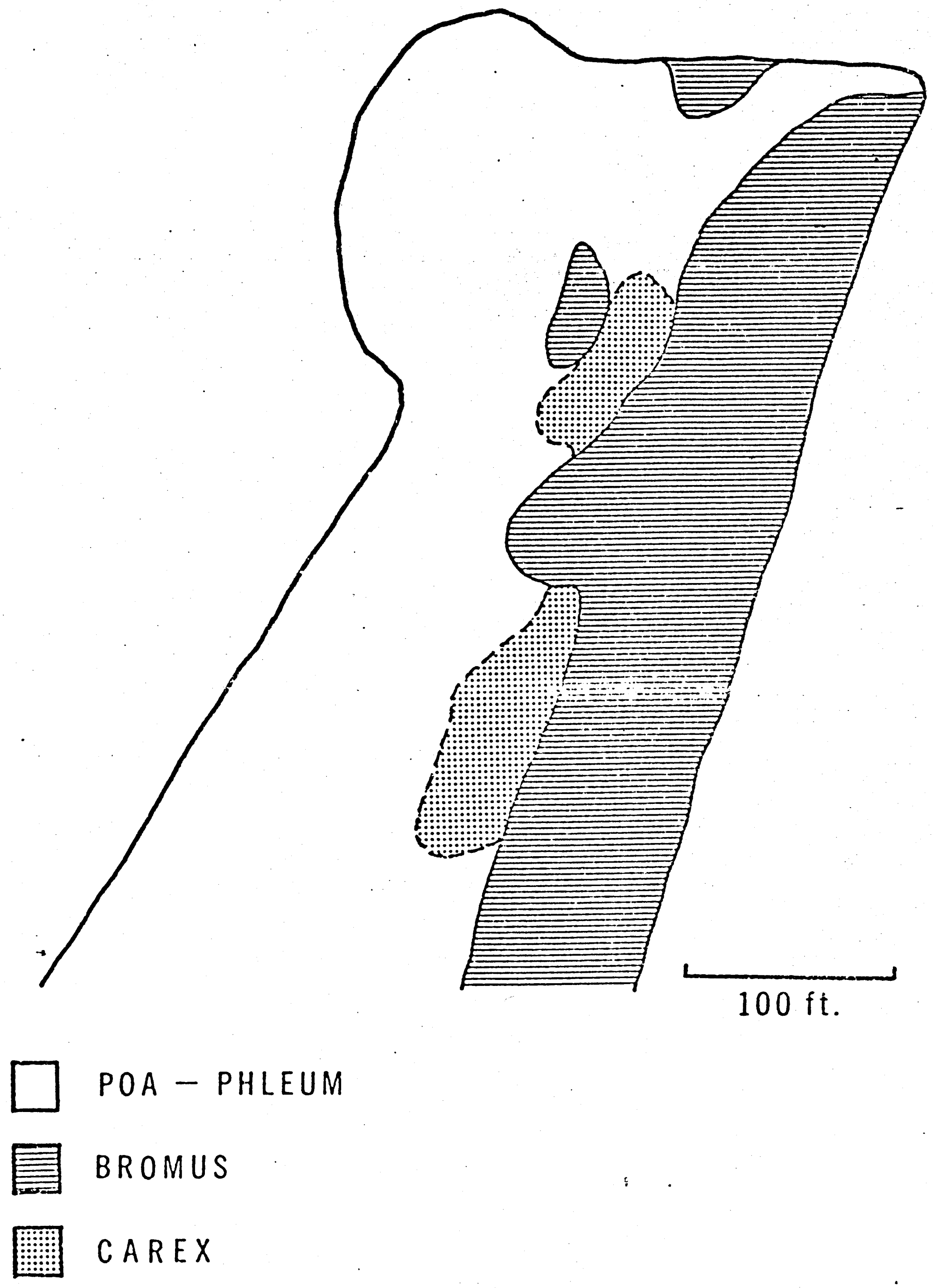

100 ft.
POA — PHLEUM
BROMUS
CAREX

Fig. 6. A portion of the sharp _Carex rosea_, _Bromus inermis_ transition.

Fig. 7. A typical portion of the jack pine stand.

inches d.b.h. and 21 feet tall. There is an almost continuous cover of brome grass (Bromus inermis) in this stand although the grass here is not as thick and the litter layer is not as deep as in the meadow. Tall meadow rue (Thalictrum dasycarpum) and early meadow rue (Thalictrum dioicum) are common herbs, and wild rose (Rosa sp.) is the most common shrub, except in the large open areas, where red raspberry (Rubus idaeus) forms an almost continuous shrub layer (Fig. 8).

The area between the mature aspen forest and the north end of the meadow is characterized by young aspens up to 5 inches in diameter forming an almost continuous canopy, a fairly heavy shrub layer of wild rose (Rosa sp.), red raspberry (Rubus idaeus), and poison ivy (Rhus radicans), and a herb layer of tall meadow rue (Thalictrum dasycarpum), early meadow rue (Thalictrum dioicum), and brome grass (Bromus inermis). The jack pine at the edge of the meadow were planted at the same time as those in the stand at the west side of the meadow (Fig. 9).

The forest lying outside of Wegmann's fenced field is now a very dense, mature aspen stand. The 11 chimneys of line 2 were used as the reference points for an evaluation of the trees (4 inches and above d.b.h.) of this stand by the point-quarter method (Cottam and Curtis, 1956; Curtis and McIntosh, 1951). The tree density is 239 trees per acre of which 207 per acre are aspen (Populus tremuloides). One of the largest aspens was found to be 66 feet tall and 11.1 inches d.b.h. The only other species seen in the point-quarter sampling were American elm (Ulmus americana), bur-oak (Quercus macrocarpa), and hard maple (Acer saccharum)

Fig. 8. A typical portion of the red pine stand.

Fig. 9. A typical portion of the young aspen part of the study area.

(Table 2). The shrub layer (woody plants between 1 and 15 feet tall) is extremely thick in the aspen stand. The percentage cover by shrubs and trees was measured by the line intercept method (Buell and Cantlon, 1950) along a 200 foot line 5 feet south (to avoid trampled brush) of line 2. Along this line the shrub cover was complete and hazelnut (Corylus americana) and beaked hazelnut (Corylus cornuta) contributed 36 and 37 percent respectively of the cover and a number of other species supplied the remainder of the cover. The tree layer was 60.5 percent aspen and 34 percent open (Table 3). A 200 foot line was also run 5 feet south of line 4 in the young aspen stand to serve in comparing the two areas. In this area the shrub layer was 78.5 percent open and the tree layer was only 9.5 percent open, with the young aspen comprising 85.5 percent of this tree layer. The most common plants in the herb layer of the mature aspen stand are Carex sp., lady fern (Athyrium felix-femina), wild lily of the valley (Maianthemum canadense), early meadow rue (Thalictrum dioicum), poison ivy (Rhus radicans), and aster (Aster macrophyllus).

Plant nomenclature used is according to Gleason and Cronquist (1963). Plant species listed in Appendix D.

A soil sample taken from the center of the northern part of the meadow was analysed by the University of Minnesota Soil Testing Laboratory. The texture of this sample was sandy loam. It had a pH of 5.9, a relatively low level of organic matter, a very high level of extractable phosphorus (34 lbs. per acre), and a low level of exchangeable potassium (70 lbs. per acre).

Table 2. Results of point-quarter tree sample taken at 11 points (44 trees) on line 2.

Mean distance	(d)	=	13.7 ft.
Mean area	(M)	=	187.7 ft.^{2}
Density	(D)	=	239 trees per acre
Mean basal area	(MBA)	=	.326 in.^{2} per tree
Basal area per acre		=	77.9 ft. per acre

	Populus tremuloides	*Ulmus americana*	*Quercus macrocarpa*	*Acer saccharum*
Relative density	86.4%	6.8	4.5	2.3
Absolute density	206.5/acre	16.3	10.8	5.5
Frequency	100%	27.3	18.2	9.1
Relative frequency	64.7%	17.6	11.8	5.9
Relative dominance	93.1%	4.4	1.8	.8
Basal area	72.5 in.^{2}/acre	3.4 in.^{2}/acre	1.4 in.^{2}/acre	.6 in.^{2}/acre
Importance value	244.2	28.8	18.1	9.0

Table 3. Tree and shrub cover on lines 2 and 4.

	Trees		Shrubs	
	line 2	line 4	line 2	line 4
Open	34.0%	9.5%	--	78.5%
Amelanchier sp.	--	--	1.0	--
Cornus stolonifera	--	--	11.5	--
Corylus americana	--	--	36.0	--
Corylus cornuta	--	--	37.0	--
Crataegus sp.	--	--	--	2.0
Pinus banksiana	--	2.0	--	--
Populus balsamifera	--	8.0	--	2.0
Populus tremuloides	60.5	85.5	--	3.0
Prunus nigra	--	--	4.5	--
Prunus pennsylvanica	3.5	--	2.0	--
Prunus serotina	--	--	--	1.0
Prunus virginiana	--	--	1.5	3.0
Quercus borealis	--	--	1.0	--
Quercus macrocarpa	2.0	--	1.5	--
Rosa sp.	--	--	--	8.5
Rubus idaeus	--	--	--	2.0
Viburnum rafinesquianum	--	--	4.0	--

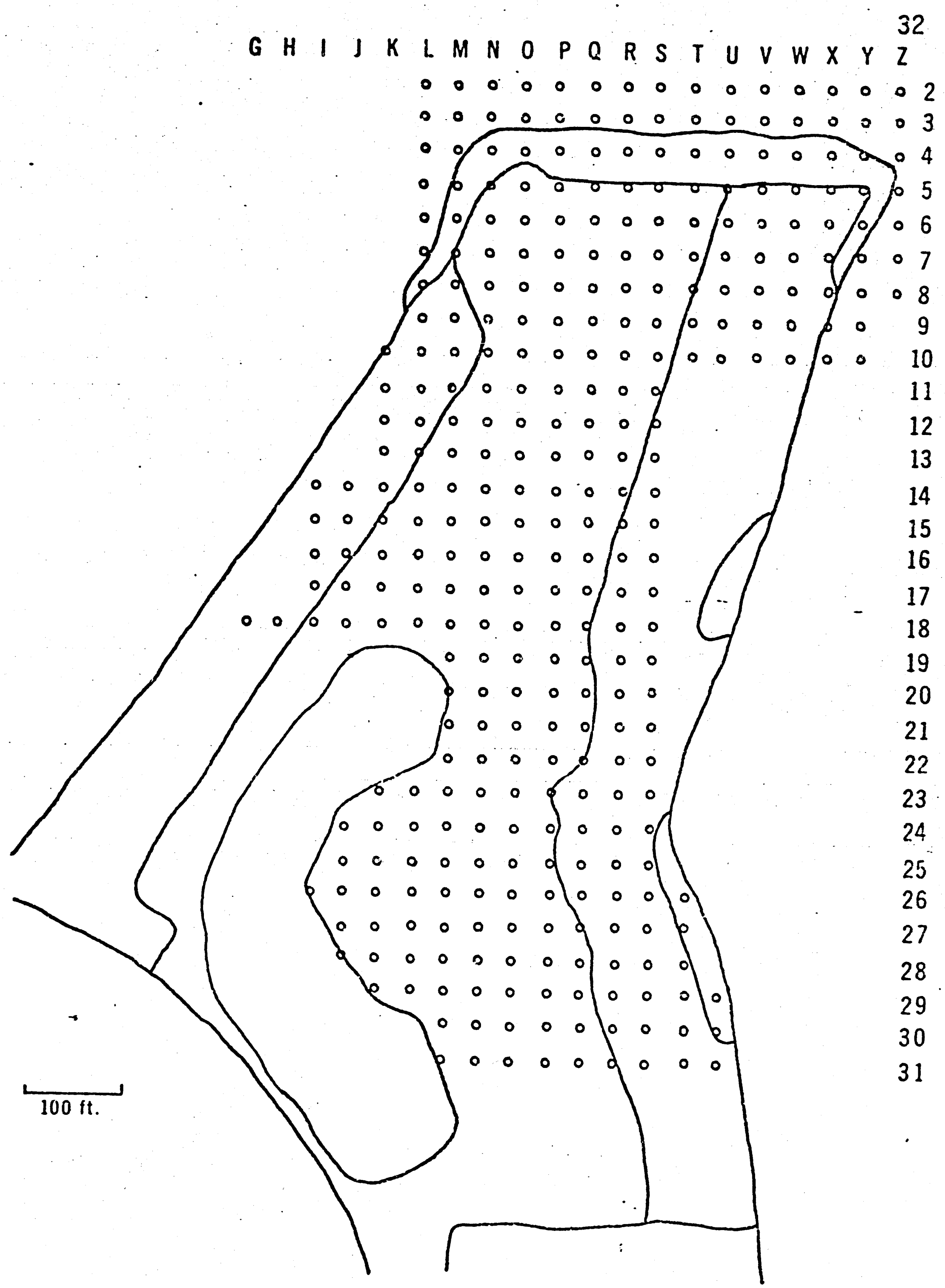
METHODS AND MATERIALS

A trapping grid was set up on the study area in 1965 with lines (numbered 1 through 31) running on an east-west magnetic heading and rows (lettered A through Z) running on a north-south magnetic heading. Stakes were set at 35 foot intervals on the portion of the grid actually trapped. Rows A through F and line 1 were never used. The stake positions are shown in Figure 10. The study area was mapped with the aid of these stakes by placing the stake positions on graph paper and placing the features of the study area on the graph in relation to the stake positions.

Trapping sessions were started the first summer of the study (1965) at the southern end of the grid, away from the primary area of interest. Trapping proceeded toward the north end of the study area during the course of the summer. This was done in order to familiarize myself with the animal species of the area and to work out procedures, particularly measuring technique, to be used for the remainder of the study. During the summer of 1965 the traps were placed by the stakes. After the chimneys were positioned in September, 1965, the traps were placed in the chimneys during the summer as well as in the winter.

During the summer trapping sessions the traps were set at 4 o'clock each afternoon and were checked and turned over at 0800 each morning. The traps were checked at 8 hour intervals during sessions starting on August 30, 1966, November 3, 1966, April 28, 1967, and August 3, 1967.

Fig. 10. The positions of the stakes placed in July, 1965.


32
G H I J K L M N O P Q R S T U V W X Y Z
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
100 ft.

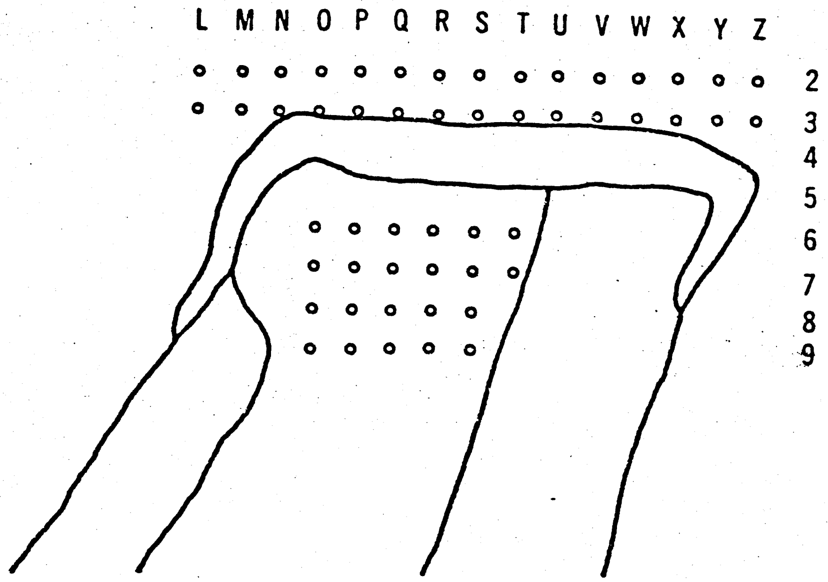
Pruitt (1959a) reported 100 percent survival during cold weather when the traps were checked every 8 hours but said that some animals did not survive 10 hour trapping periods. The latter finding was confirmed during the first winter trapping session in 1966 when several animals were found dead in traps after an all night trapping period. Therefore, for the remainder of the study during all trapping sessions from November to April inclusive, the traps were set at the beginning of each session and were checked at 8 hour intervals (0800, 1600, 2400).

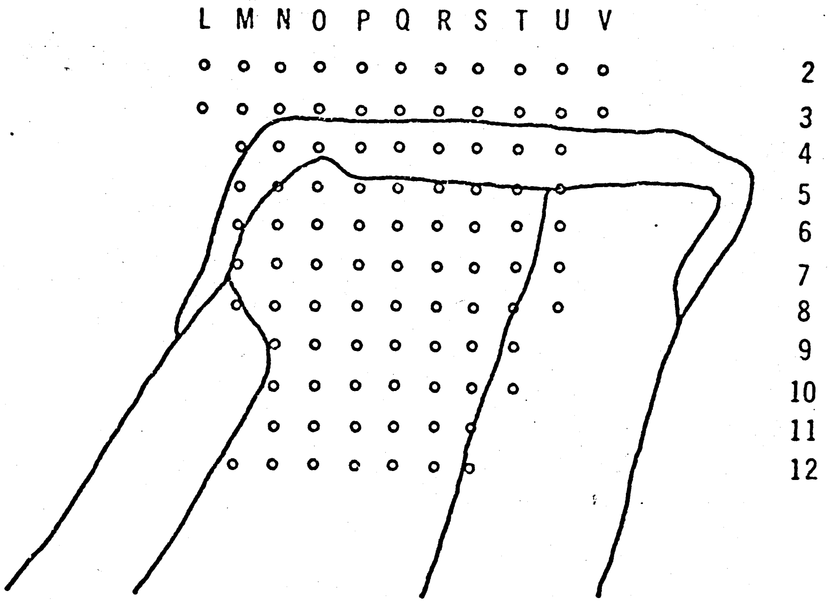
On September 16-17, 1965, 52 chimneys were placed in the study area on lines 2, 3, 6, 7, 8, and 9 (Fig. 11). The litter was cleared away from the area next to each stake where a chimney was to be placed but the sod mat was not disturbed. An effort was made to disturb the area as little as possible when positioning each chimney. All chimneys were turned so that the open end in the bottom faced north. The chimneys were positioned this way because winds from the north are cut off by the trees at the north end of the meadow and also because the trails used during the first summer ran along the lines to the south side of the stakes. An effort was made during the entire study to use the same trails and to step next to the chimneys only on the south side. Between June 21 and 29, 1966, 8 of the original 52 chimneys were repositioned and 42 additional chimneys were added. These 94 chimneys constituted the grid used for the remainder of the study (Fig. 12).

Several modifications were made to the chimneys as described by Pruitt (1959a). The 4 foot height needed in Alaska was thought

Fig. 11. Positions of the chimneys during the first winter of the study (January-March, 1966).

Fig. 12. Positions of the chimneys during the remainder of the study (June, 1966-March, 1968).


L M N O P Q R S T U V W X Y Z
2
3
4
5
6
7
8
9


L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12

to be unnecessary in Minnesota and the chimney height was reduced to 2 feet 8 inches. Cutting the sides to the dimensions of 2 feet 8 inches by 12 inches and 2 feet 8 inches by 6 inches also gives efficient utilization of standard 4 foot by 8 foot sheets of plywood. Five-eights inch plywood was found to be unnecessarily thick for the shortened chimneys and the last 76 chimneys were constructed of 3/8" plywood. The hook and eye method used by Pruitt to hold the hinged tops down was found to be very slow to use while wearing mittens. Darby Nelson, a fellow graduate student, suggested that a small nail be driven through the top of each chimney and a short distance into the side wall to serve as a kind of friction catch. A hand axe was used as a wedge to open the tops while a firm push was sufficient to reseal them. Figure 13 shows two views of chimneys in position on the meadow.

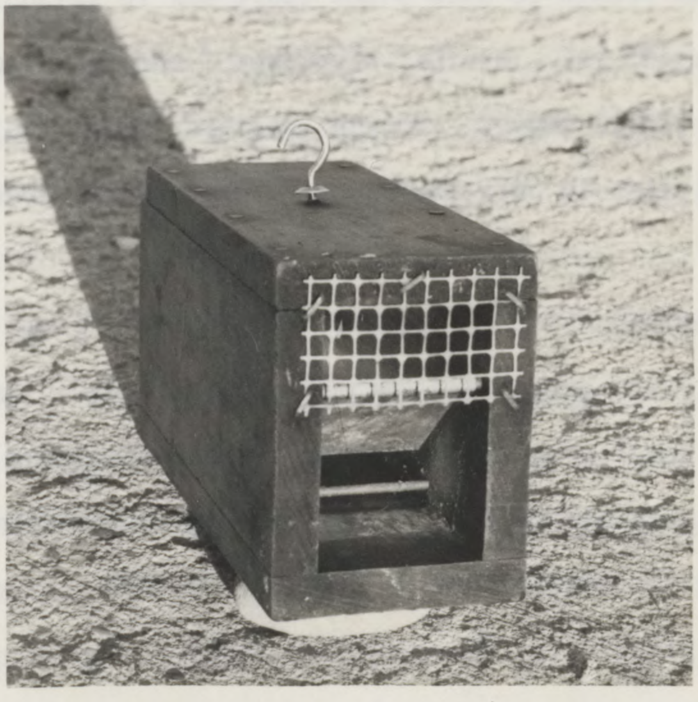
The traps used were wooden, multiple catch traps of the type described by Gunderson and Beer (1953, pp. 13-14). They are constructed of 1/2" redwood and have inside dimensions of 1 3/4" x 2 3/4" x 7 1/2" (Fig. 14). The trapping mechanism consists of an aluminum door sloping inward at the bottom and hinged by a pin 1" from the top of the trap. Hardware cloth (1/4" mesh) covers the opening above the hinge. A sliding aluminum door at the back of the trap is used for removal of captured animals. The traps were borrowed from the Bell Museum of Natural History and were the same traps used by Frenzel (1957) in a study of small mammals on an island in Basswood Lake, Minnesota. The only modification required to adapt these traps for use in the chimneys was the addition of one cup hook screwed into the center of the top of

Fig. 13. Two views of chimneys in place in the meadow. The lower photograph shows the opening at the bottom of the chimney.

Fig. 14. One of the live-traps used in the study.

Fig. 15. A modified live-trap with the nail modification visible.


UNIVERSITY OF MINNESOTA BOOKSTORES



each trap. It was discovered that the use of two cup hooks, as suggested by Pruitt (1959a) was unnecessary. In fact one hook proved to be faster to catch and also easier to manipulate at the end of the pickup rod.

Traps of this type have the advantages of being easy on trapped animals due to the wooden construction, and simplicity of the trapping mechanism which is set automatically whenever the trap is upright and is not set when the trap is in any other position. Both are assets particularly important in the winter.

On the other hand this type of trap has been criticized because of, 1) the possibility of multiple captures, with the attendant risk of animals hurting or killing each other (Blair, 1941b), and 2) the ability of some animals to escape from this type of trap (Gunderson and Beer, 1953, p. 13). The first criticism proved to be of comparatively small consequence. During the course of the study there were 39 double captures, 5 triple captures, and 1 quadruple capture. Yet there were only 5 cases of one animal hurting another. Sheppe (1967) reported 25 double and 2 triple captures with no sign of animals hurting each other.

It is true, however, that some animals can escape from this type of trap. Occasionally, *Blarina brevicauda* scats, *Peromyscus* sp. scats, and *Clethrionomys gapperi* scats were found in empty traps. (There was never any indication that *Microtus pennsylvanicus* could escape from the traps.) A modification of the traps to cure this problem was suggested by Dr. William Schmid of the Zoology Department of the University of Minnesota and by Mr. Oscar

Kalin of the Bell Museum of Natural History. A nail was driven through the sides of each trap 1/4" from the floor and just far enough back from the front so that the hinged door just cleared the nail (Fig. 15). The traps were all modified by February 22, 1967 and no evidence of animals escaping was seen thereafter.

No nesting material was used at any time in these traps. Pruitt (personal communication) said that in his experience with the chimney technique nesting material was "worse than useless" and felt that it is much more important to keep sufficient food in the traps and to check them often than to introduce nesting material.

A mixture of oatmeal and peanut butter mixed in approximately equal proportions by weight was used to bait the traps. Beer (1964) tested a number of baits and found this mixture to be the most effective bait for a variety of small mammals. The granulated texture of this mixture also proved to be convenient to handle. A sufficient amount of bait was placed in each trap (approximately a level tablespoon) to insure an excess above the needs of several animals in case of multiple captures.

Each animal captured was taken to a central area for weighing, measuring, and examination. A styrofoam ice chest was used to carry the animals, in the traps, to the examining station and back to the chimneys, where captured, for release. In the summer this examining station was simply a spot on the meadow where the equipment was kept under a tarpaulin. In the winter a small canvas ice fishing house was used as a field station.

At the first capture each animal was toe-clipped and ear-notched for identification. The back toes were used as units, the front toes as tens, and each ear as an additional hundred. Each species was numbered separately. Prior to August 31, 1966 each animal was weighed and measured after each capture. There were sufficient data by that time to judge the reliability of the measuring technique and after that date each animal was weighed and measured only once during any one trapping session. Animals were weighed in a glass jar on an Ohaus triple beam pan balance to the nearest half gram. Total length, tail length and hind foot length were measured directly in millimeters. Body length was calculated by subtracting tail length from total length. Since I was inexperienced at handling small live mammals at the beginning of the study, and also because the measuring technique was modified several times during the early part of the first summer of trapping, no linear measurements taken prior to August 5, 1965 have been used. The following measurement technique was used for the remainder of the study.

Total length

The measuring board was placed with the end board to the left. A glove was worn only on the right hand. The animal was grasped behind the neck with the thumb and forefinger of the right hand and held firmly against the measuring board with its nose lightly touching the end board. By reaching under the right hand, the tail was grasped near its tip with the thumb and forefinger of the left hand and the tail was pulled with sufficient force to insure that the animal was not shortening the measure by tensing its muscles.

Tail length

The animal was held behind the neck with the right hand and turned ventral side up. The animal's tail was bent down over a thin plastic ruler held perpendicular to the animal's body, and both the ruler and tail were simultaneously grasped between the thumb and forefinger of the left hand. The tip of the ruler was vertically in line with the posterior edge of the anus. The tail was measured to the tip of the skin of the tail.

Hind foot length

The animal's left hind foot and the thin plastic ruler were simultaneously grasped between the thumb and forefinger of the left hand so that the ankle was perpendicular to the ruler and the heel was even with the edge of the ruler. The foot was measured to the tip of the nails.

The temperature on the study area was measured by means of a Taylor Maximum-Minimum Thermometer and a Tri-R Model TSB Electronic Thermometer. During the summer of 1965 the maximum-minimum thermometer was placed in the litter near grid position 6-T. From September 1965 through the remainder of the study this thermometer was kept in the bottom of the chimney at 6-T. The maximum and minimum temperatures were recorded every time the traps were set or checked. Thermister probes were first placed in the area on February 22, 1967. One probe was placed at ground level, another at 20 cm. above the ground, and a third at the surface of the snow. The first two probes were placed by taping them into a shallow groove in the side of a long, narrow stick and carefully pushing the stick into the snow between 6-T and 7-S. The third probe was movable in the groove and its position was moved to coincide with the snow surface. Another probe was placed in the bottom of chimney 6-S. During the snow-free trapping sessions in 1967 the probes at ground level, at 20 cm. above ground level, and in chimney 6-S were used, and in addition one probe was placed in chimney 3-U and another in the litter near 3-U. The electronic thermometer itself was carried to and from the study area in the ice chest used to carry the traps. Temperatures were taken every time the traps were set or checked.

Snow depth was measured with a meter stick in the area between 6-T and 7-S.

The nomenclature used for all mammalian species is according to Gunderson and Beer (1953).

DISTRIBUTION

Results

June - September, 1965

The initial trapping during the first summer of the study was designed to sample a large portion of the meadow and extensive areas of the adjacent habitats for species distribution. The position of all captures and recaptures during this first summer (July 1 - September 17, 1965) are shown in Figures 16, 17, and 18.

It appears that most of the small mammal species were strongly restricted to certain habitats and/or strongly excluded from other habitats. The meadow mouse (Microtus pennsylvanicus) was the principal species trapped in the meadow and in the red pine habitats (Fig. 16). The latter species was not trapped in any other habitat. The only other animals caught in the meadow were a thirteen-lined ground squirrel (Citellus tridecemlineatus), two Franklin ground squirrels (C. franklinii), one eastern chipmunk (Tamias striatus), and a jumping mouse (Zapus hudsonius) (Figs. 17, 18).

The principal species trapped in the mature aspen were the red-backed vole (Clethrionomys gapperi), the eastern chipmunk, and the deer mouse (Peromyscus sp.) (Figs. 16, 18). The deer mice were of the Peromyscus maniculatus maniculatus - Peromycus leucopus noveboracensis type and could not be definitely assigned to one subspecies or the other on the basis of any characteristic or

Fig. 16. Distribution of captures of *Microtus pennsylvanicus* ○, *Clethrionomys gapperi* □, and *Peromyscus* sp. ⬢ from July 1, 1965 to September 17, 1965.

1 capture	○	□	⬢
2 captures	○	□	⬢
3 captures	○	□	

4 or more captures indicated by numeral in figure.

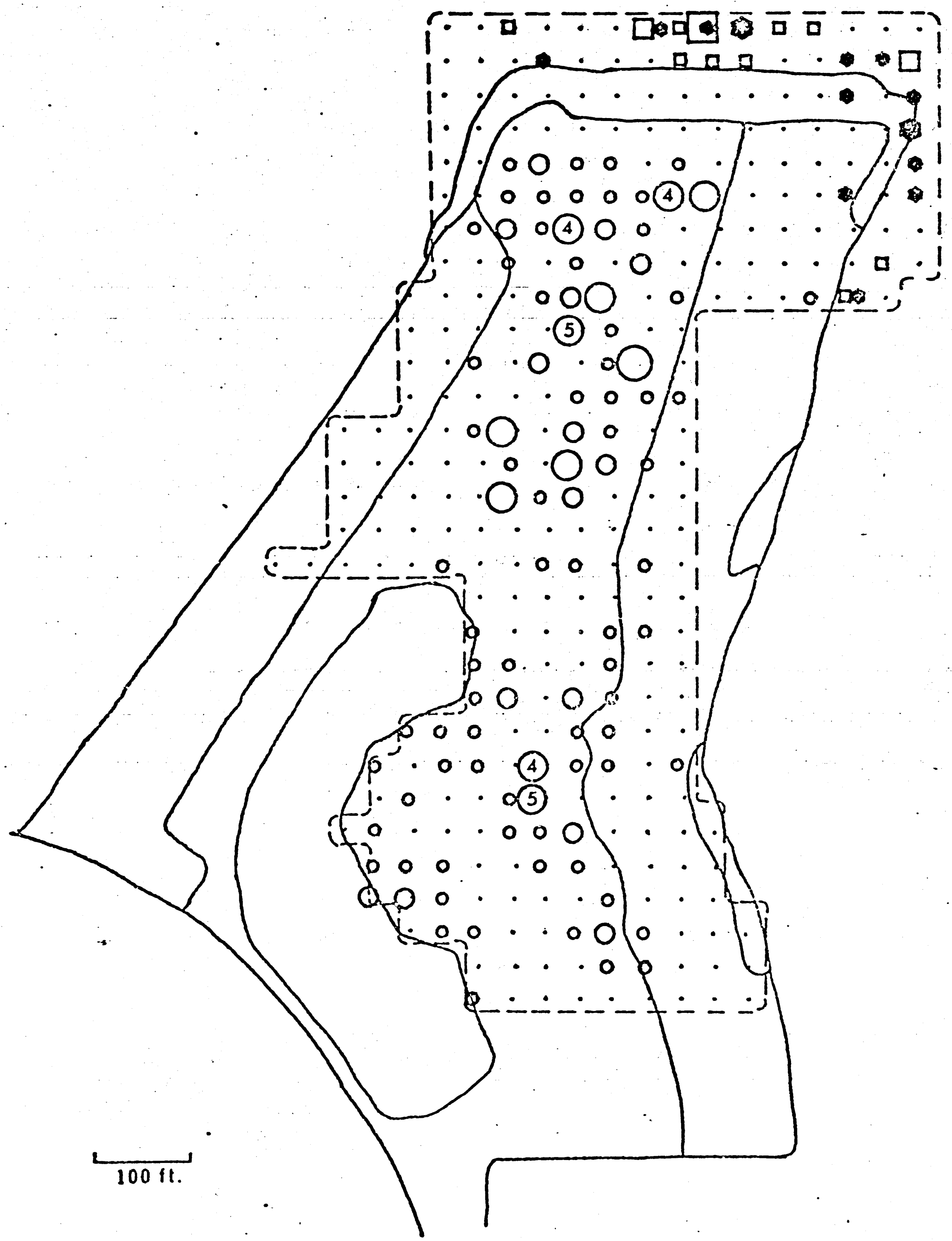

4
4
5
4
5
100 ft.

Fig. 17. Distribution of captures of *Blarina brevicauda* △, *Sorex cinereous* ○, *Zapus hudsonius* □, and *Synaptomys cooperi* ⬢, from July 1, 1965 to September 17, 1965.

1 capture	△	○	□	⬢
2 captures	△			

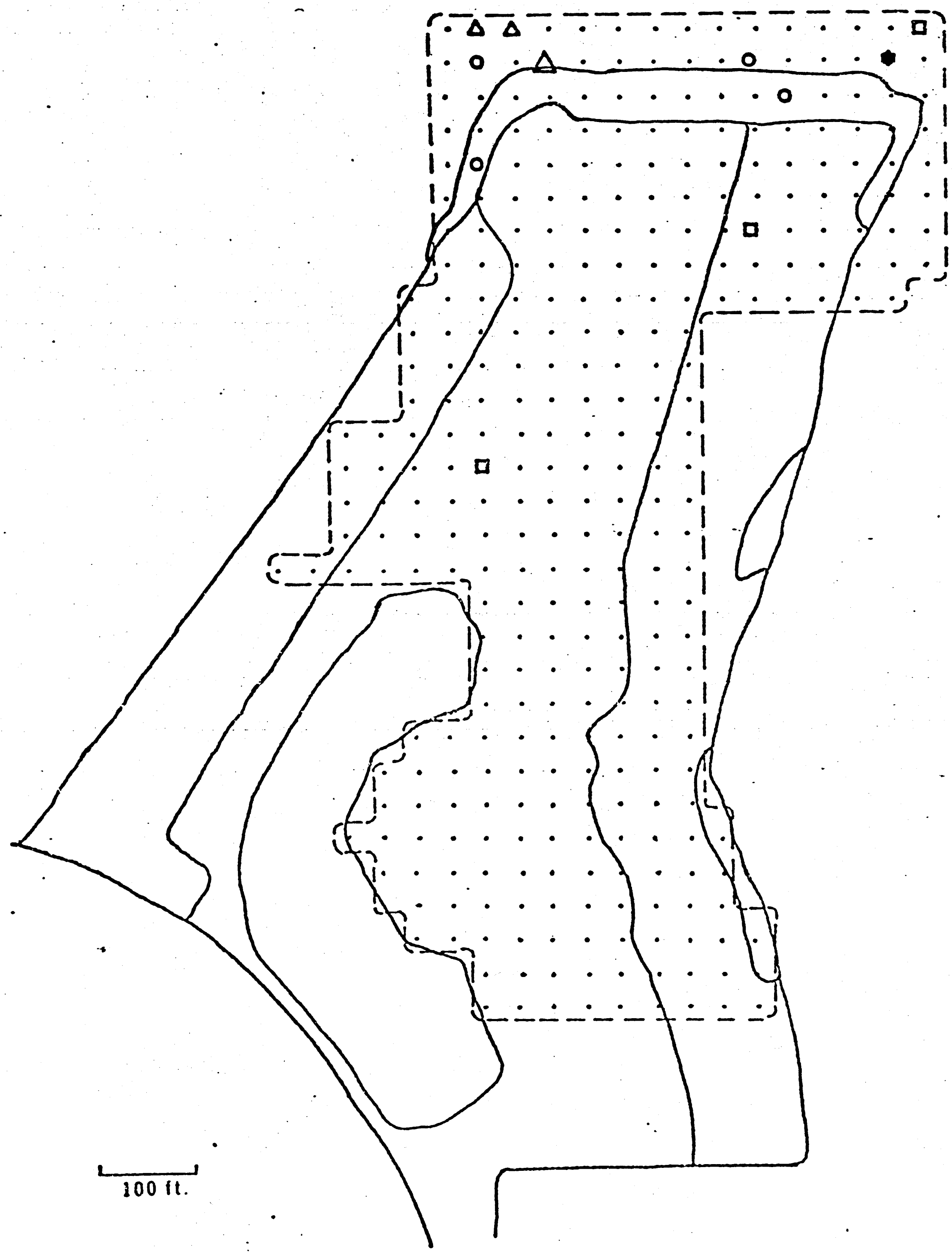
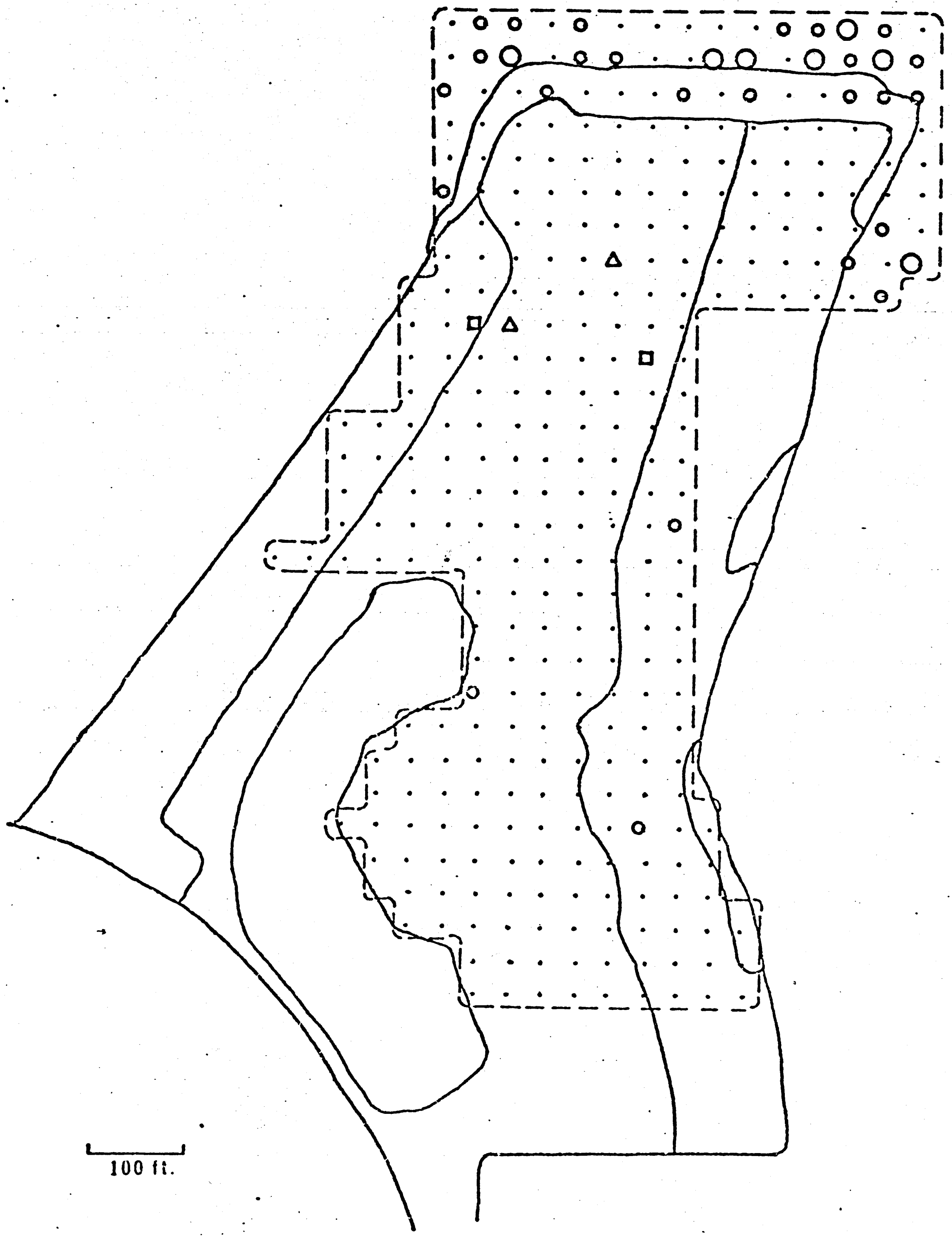

100 ft.

Fig. 18. Distribution of captures of <u>Tamias striatus</u> ○, <u>Citellus tridecemlineatus</u> △, and <u>Citellus franklinii</u> □, from July 1, 1965 to September 17, 1965.

1 capture ○ △ □

2 captures ○


100 ft.

or combination of characteristics. Hnatiuk and Iverson (1965) studied *P. maniculatus bairdii*, *P. maniculatus gracilis*, and *P. leucopus noveboracensis* taken from the ecotone region of northeastern North Dakota and northwestern Minnesota, and demonstrated overlap of morphological characters so that a single set of measurements could not be reliable for definite identification. On the basis of the morphological intergrades found, Iverson, et al (1967) suggest that gene exchange may have taken place between the subspecies of deer mice found in this ecotone. There were also several captures of short-tailed shrews (*Blarina brevicauda*), and common cinereous shrews (*Sorex cinereous*)(Fig. 17). The only capture of a bog lemming (*Synaptomys cooperi*) during the entire study was made in the mature aspen during the first summer (Fig. 17).

Comparatively few captures were made in the young aspen during the first summer. Eastern chipmunks appeared to use this area regularly (Fig. 18), and two of the four cinereous shrews captured were taken in the young aspen habitat.

Four points should be mentioned which are illustrated by the distribution diagrams of the first summer's trapping. First, a population of meadow mice appeared to have the meadow virtually to themselves insofar as the small, winter-active, mammals are concerned. Second, populations of red-backed voles and deer mice were taken only in the mature aspen and apparently were restricted to that habitat. Third, not only was there no overlap between these field and wood species but there was a zone approximately 70 feet wide between them where neither voles nor mice were trapped. Fourth, no animals were trapped in the jack pine habitat during 250 trap nights of effort in that area.

January - March, 1966

The 52 chimneys available for use during the first winter were positioned on September 16-17, 1965 (Fig. 11). They were placed in these positions, on the basis of the results of the summer trapping, to make maximum use of trap time while at the same time sampling both meadow habitat and adjacent mature aspen habitat.

The position of all captures during the January - March, 1966, period are shown in Figure 19. Although the sample size was small it appeared that there was no major shift in habitat for any of the three species captured. One meadow mouse was captured in the mature aspen and one short-tailed shrew was captured in the meadow. The meadow mouse captured in the mature aspen proved to be the only one taken in the mature aspen habitat during the entire course of the study. No deer mice were captured during the first winter.

June - November, 1966

In June, 1966, the positions of some chimneys were changed and additional chimneys were added (Fig. 12). No further changes were made in the area trapped for the remainder of the study.

The positions of captures of the winter-active species during the snow-free trapping sessions of 1966 are shown in Figure 20. The trapping results during this season indicate

Fig. 19. Distribution of all captures from January to March 1966 (*Microtus pennsylvanicus* ○, *Clethrionomys gapperi* □, and *Blarina brevicauda* △).

1 capture ○ □ △

2 captures ○

3 captures ○

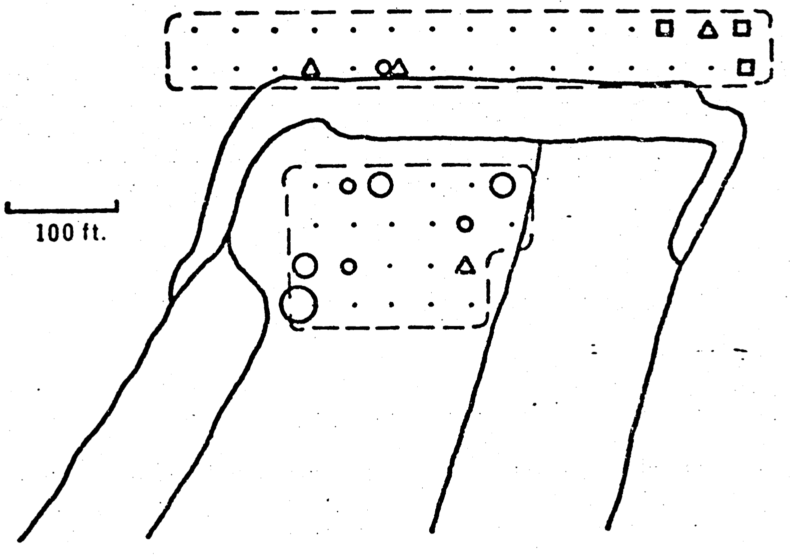
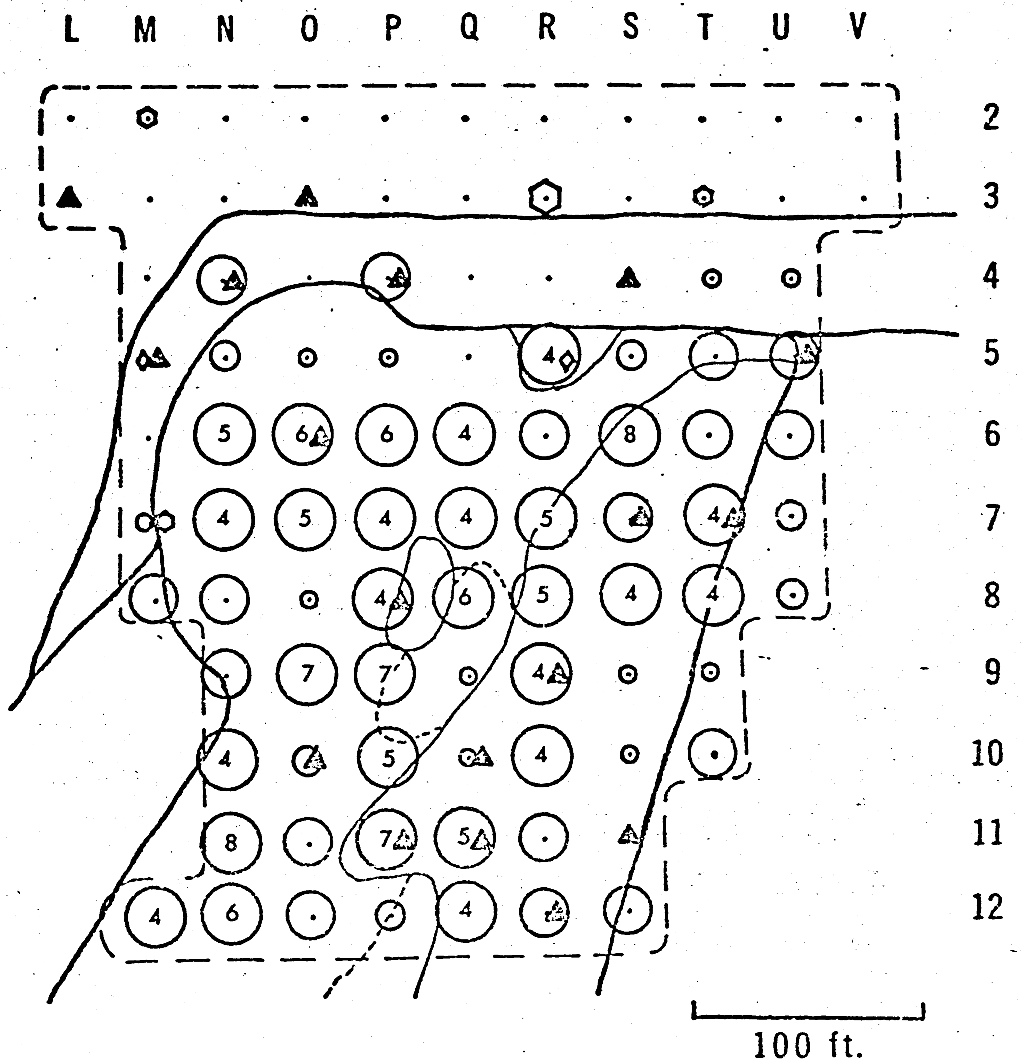

100 ft.

Fig. 20. Distribution of captures of all winter-active mammals trapped during the period June-November, 1966.

	1	2	3	4 or more
Microtus pennsylvanicus	○	○	○	○
Blarina brevicauda	▲			
Peromyscus sp.	⬡	⬡		
Sorex cinereous	◇			


L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12
100 ft.

that the meadow mice were still concentrated in the meadow. Several changes in distribution patterns from the previous summer were evident. During the summer of 1966 meadow mice were captured on line 5 at the northern edge of the meadow and a few captures were made in the young aspen. Meadow mice were also captured in the red pine habitat more frequently than would have been expected on the basis of the previous summer's trapping. It is impossible to determine from these data if meadow mice used the entire width of the red pine habitat during the snow-free portion of 1966 but it is obvious that the part of pine habitat immediately adjacent to the meadow was used extensively. A single capture of a meadow mouse at the eastern edge of the pine habitat in 1965 (Fig. 16) may indicate that the entire width of the habitat was used to some extent.

With the exception of one capture in the young aspen, the few deer mice captured were in the mature aspen. No red-backed voles were captured during the snow-free season of 1966.

Short-tailed shrews first appeared in the meadow during the 1966 season. The first sign of these shrews in the meadow was observed on July 30 when Blarina scats were found in several traps. On August 6 and 7 scats were again found in empty traps and on August 8, 4 short-tailed shrews were captured in the meadow. Since only one short-tailed shrew had been captured prior to this during the 1966 season, their appearance on the meadow was unexpected and there was no apparent indication of their place of origin.

During the early part of the summer 10 eastern chipmunks were repeatedly trapped in the mature and young aspen. A large percentage of these chipmunks were trapped every night that traps were set in these habitats, thereby rendering a number of traps out of commission for mice and voles. For this reason chipmunks were removed from the study area starting on July 12. A total of 18 chipmunks were removed from the study area during the remainder of the snow-free season.

January - March, 1967

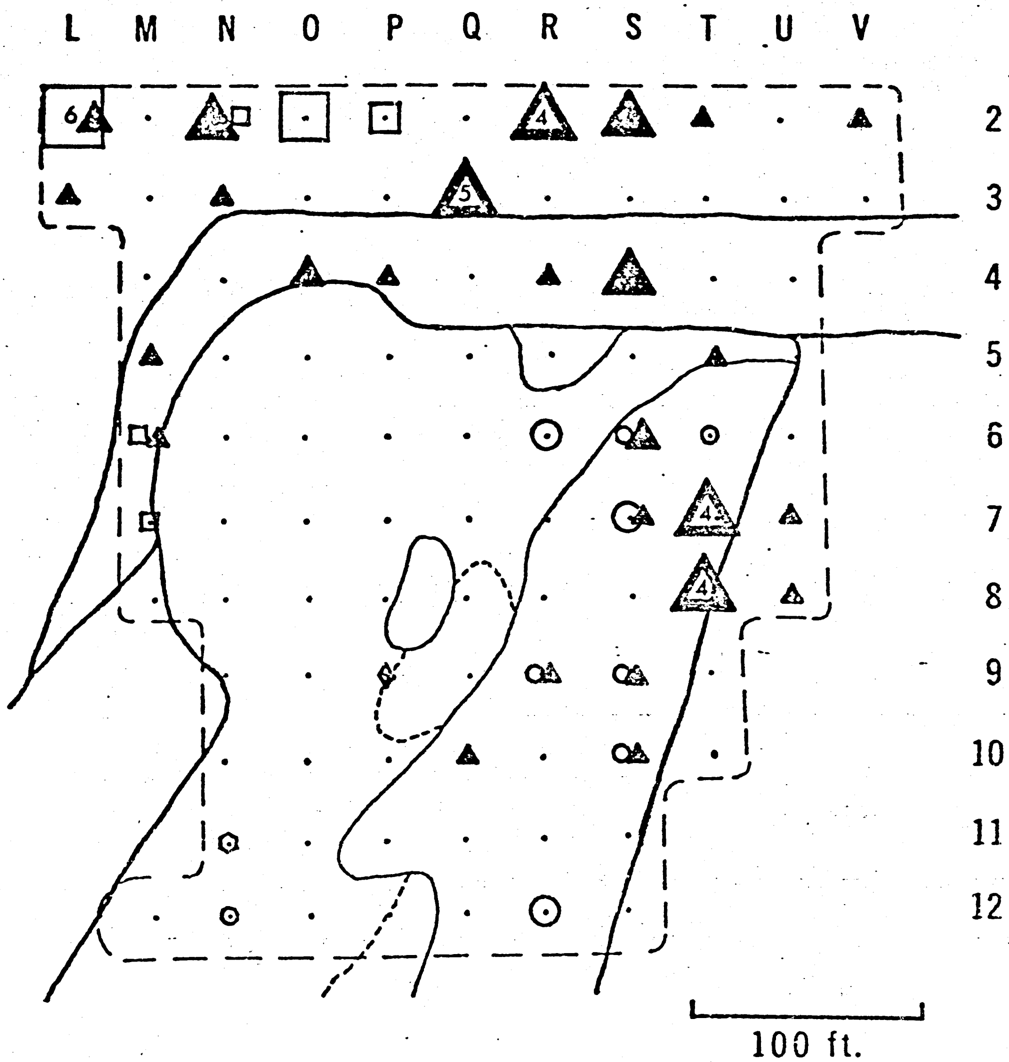
The distribution of all captures during the period January - March, 1967 is shown in Figure 21. All captures of meadow mice during this period were made in the meadow and all but one were in the eastern, Bromus, side of the meadow. The remains of a meadow and a red-backed vole were found in an unset trap (4-N) in the young aspen when the traps were first set in January. These animals could have entered this trap any time after November 5. All but one of the meadow mouse captures were made in January. After January no meadow mice were captured until March 17, the last day of winter trapping.

Red-backed voles were again, based on captures, limited to the mature and young aspen.

One deer mouse was captured in the meadow on March 16. This capture was the only one of a deer mouse during any of the winter season sessions. No other deer mouse was captured farther in the meadow (35 feet) than this particular mouse which had not been captured before and was not captured again.

Fig. 21. Distribution of captures of all winter-active mammals trapped during the period January-March, 1967.

	1	2	3	4 or more
Microtus pennsylvanicus	○	○		
Blarina brevicauda	▲	▲	▲	△
Clethrionomys gapperi	□	□	□	□
Peromyscus sp.	⬡			
Sorex cinereous	◇			


L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12
6
4
5
4
4
4
100 ft.

Short-tailed shrews were captured in all of the main habitat types during the 1967 season but in the meadow they were only trapped in the eastern, Bromus, dominated portion of the meadow. Thus the two species which used the meadow extensively, meadow mice and short-tailed shrews, were apparently concentrated in the eastern portion of the meadow.

April - October, 1967

The distribution of all captures of the small, winter-active mammals during this season is shown in Figure 22. The distribution of meadow mice during the 1967 snow-free season was very similar to that of the previous year, i.e. the mice used the meadow and red pine habitats extensively, the young aspen much less extensively, and the mature aspen not at all.

Red-backed voles were captured primarily in the mature aspen again but there were 4 captures in the young aspen and one capture at the meadows edge. These were the first and only captures of red-backed voles outside of the mature aspen during any snow-free trapping sessions.

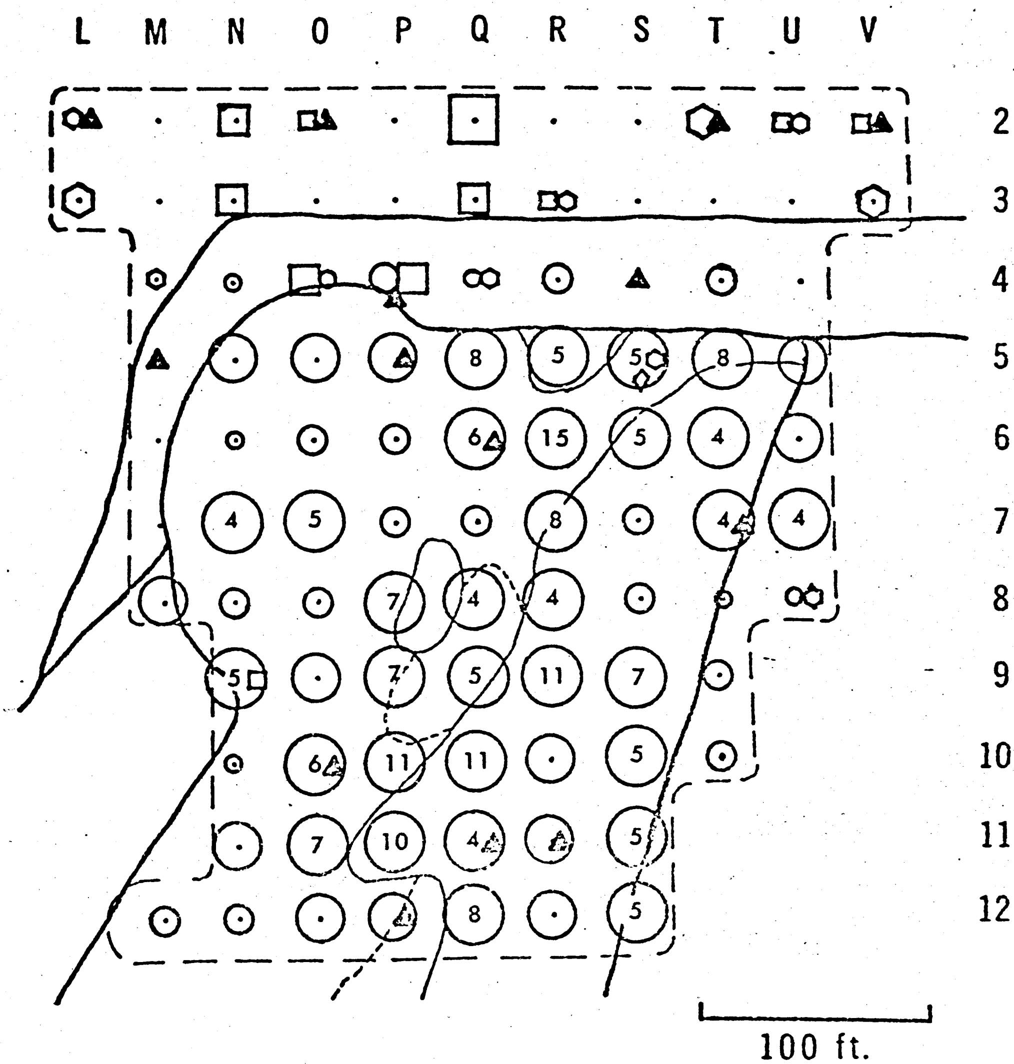
Ten of the 13 deer mice captures were in the mature aspen. One deer mouse was captured in the red pine habitat, one was captured at the edge of the meadow, and one was captured in the young aspen.

Short-tailed shrews were again captured in each of the major habitats except the red pine habitat.

During the course of this season 19 eastern chipmunks were trapped in the mature and young aspen and were removed from the

Fig. 22. Distribution of captures of all winter-active mammals trapped during the period April-October, 1967.

	1	2	3	4 or more
Microtus pennsylvanicus	○	○	○	○
Blarina brevicauda	▲			
Clethrionomys gapperi	□	□	□	□
Peromyscus sp.	⬡	⬡		
Sorex cinereous	◇			


L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12
100 ft.

study area.

January - March, 1968

The distribution of all captures during this season is shown in Figure 23. In the winter of 1968, as in the previous winter, there were no captures of meadow mice in the mature, young aspen or red pine habitats. Within the meadow the meadow mice were again primarily restricted to the *Bromus* dominated portion of the meadow.

The red-backed voles were captured in the same corner of the mature aspen and young aspen as during the previous winter.

The 3 short-tailed shrew captures were in the *Bromus*, red pine side of the study area as was the case the previous winter.

Summary and analysis of distribution

Figures 24, 25, 26, and 27 present the distribution of captures of the 4 principal winter active species from June 1966 to March 1968, by species and season. The picture of species distribution presented by these figures is generally very sharp and clear cut. Meadow mice, for example, were not found in the mature aspen during either season, and red-backed voles and deer mice were not found in the meadow during either season. Some aspects of distribution are not so easily determined by an examination of these figures, however. One would like to know if a species was equally distributed over the habitats where it was trapped or if it was more concentrated in one habitat. Were meadow mice, for example, more concentrated in the meadow during

Fig. 23. Distribution of captures of all winter-active mammals trapped during the period January-March, 1968.

	1	2	3
Microtus pennsylvanicus	○	○	○
Blarina brevicauda	▲		
Clethrionomys gapperi	□	□	
Sorex cinereous	◇		

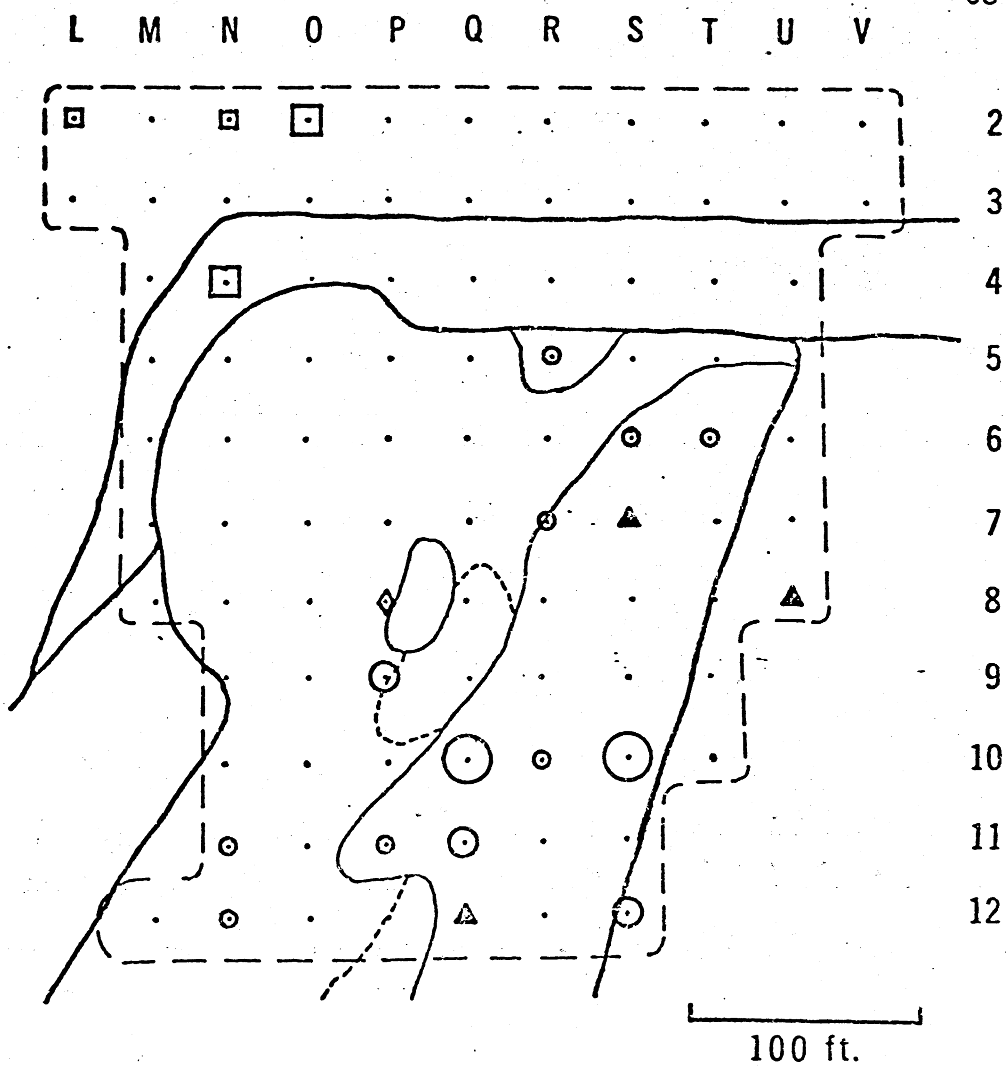

L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12
100 ft.

Fig. 24. Distribution of <u>Microtus pennsylvanicus</u> captures, June, 1966-March, 1968.

	1	2	3	4 or more indicated by numerals
Snow-free months (April-Nov.)	○	○	○	
Winter months (Jan.-March)	●	●	●	

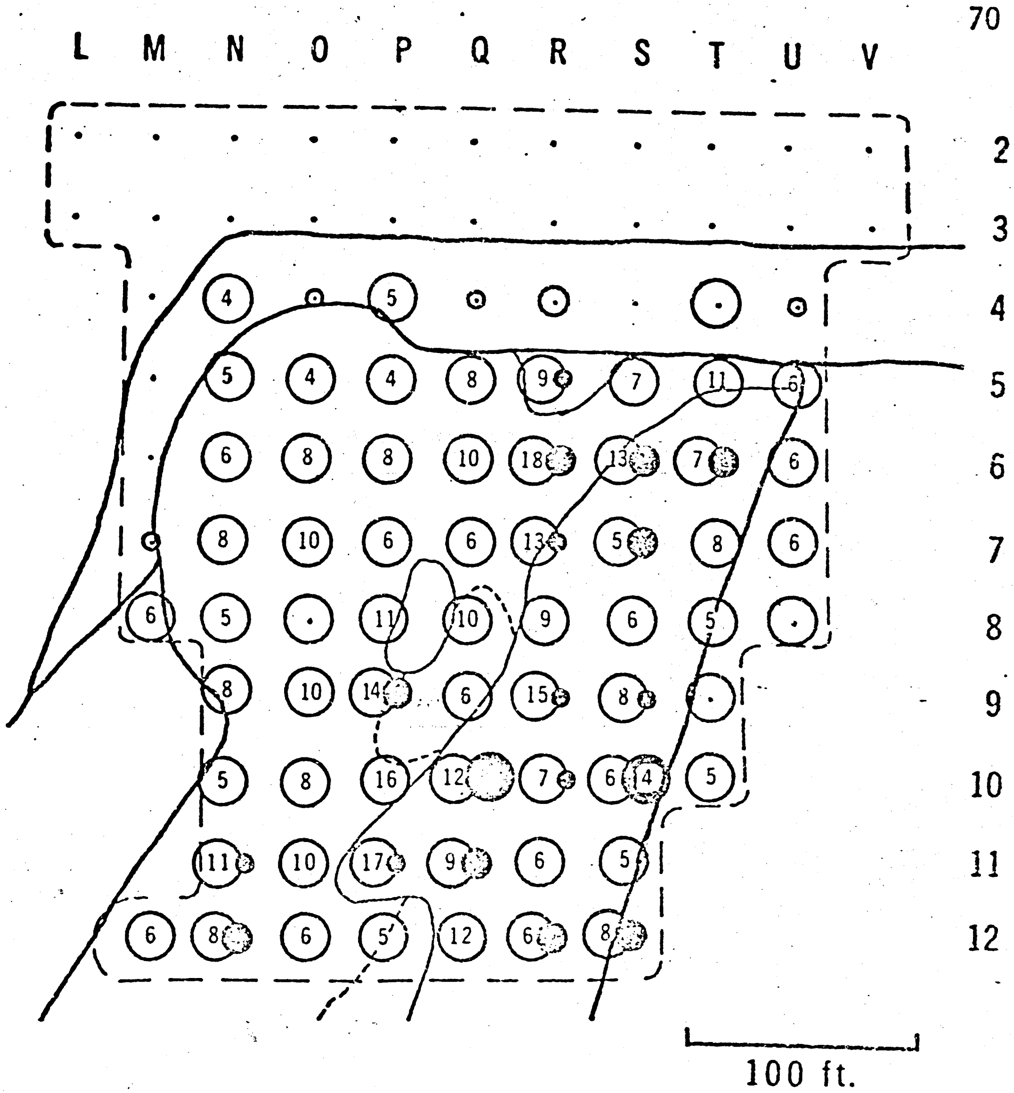

L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12
100 ft.

Fig. 25. Distribution of *Clethrionomys gapperi* captures, June, 1966-March, 1968.

	1	2	3	4 or more indicated by numerals
Snow-free months (April-Nov.)				
Winter months (Jan.-March)				

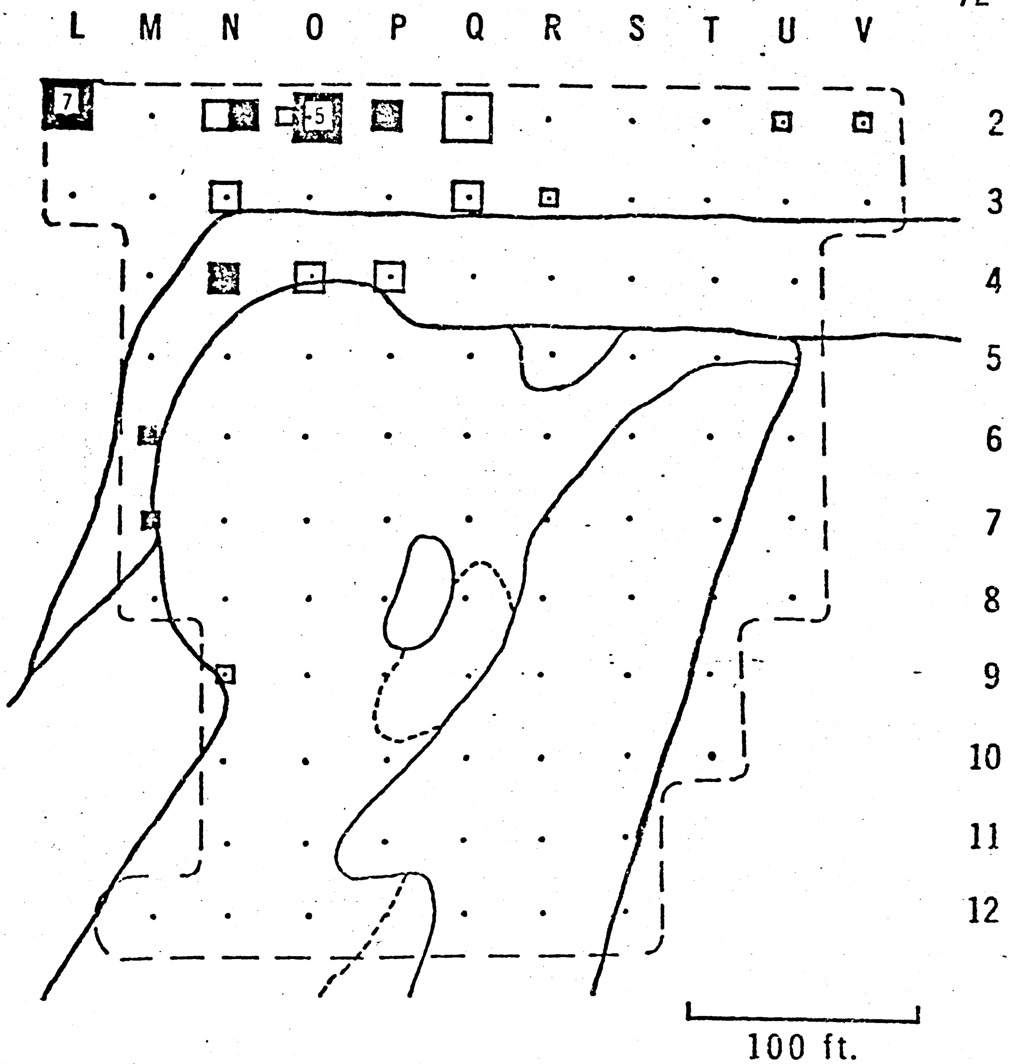
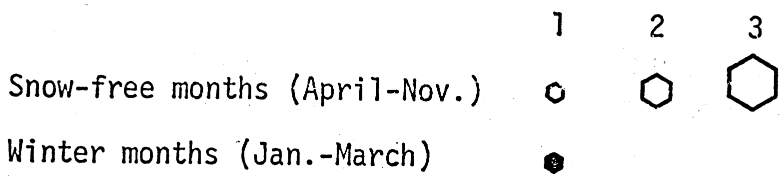

L M N O P Q R S T U V
7
-5
2
3
4
5
6
7
8
9
10
11
12
100 ft.

Fig. 26. Distribution of <u>Peromyscus</u> sp. captures, June, 1966-March, 1968.



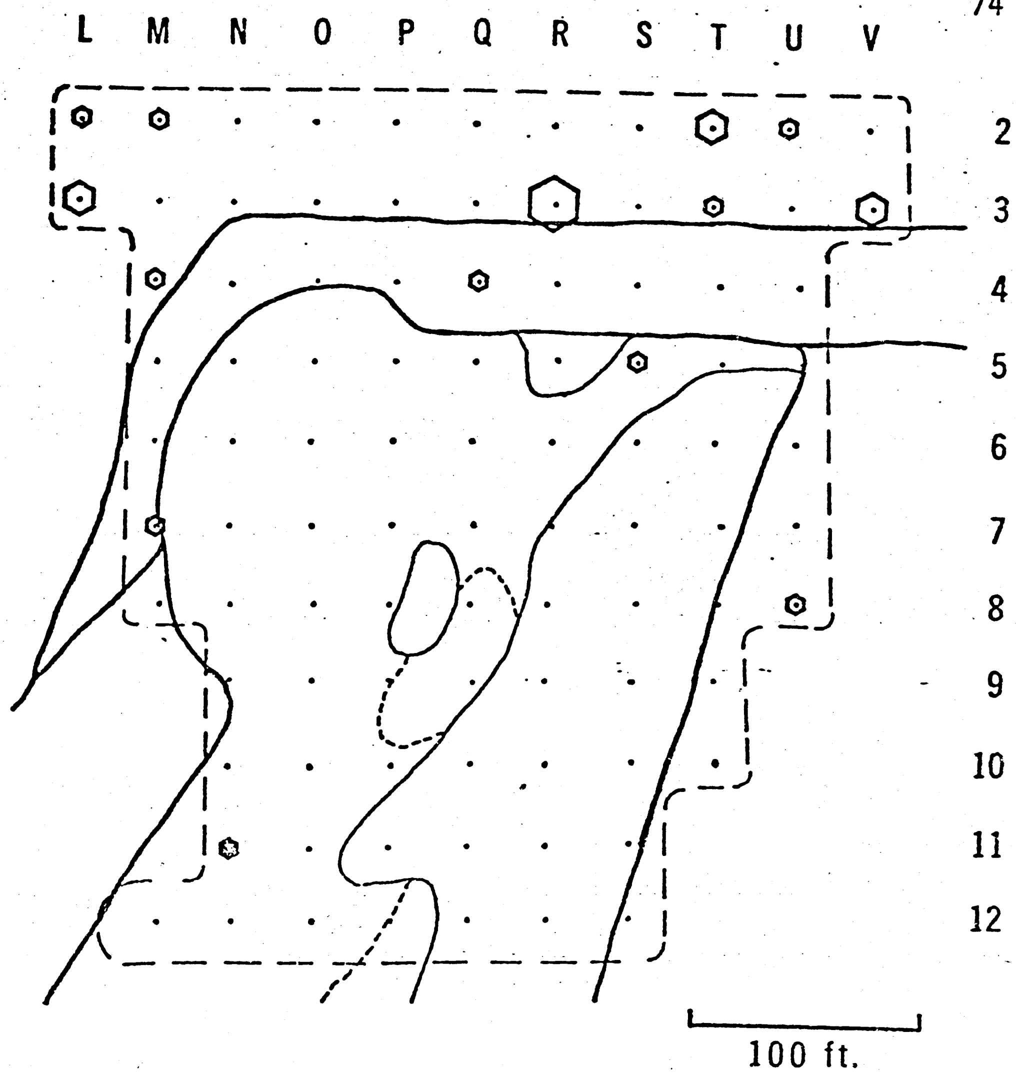
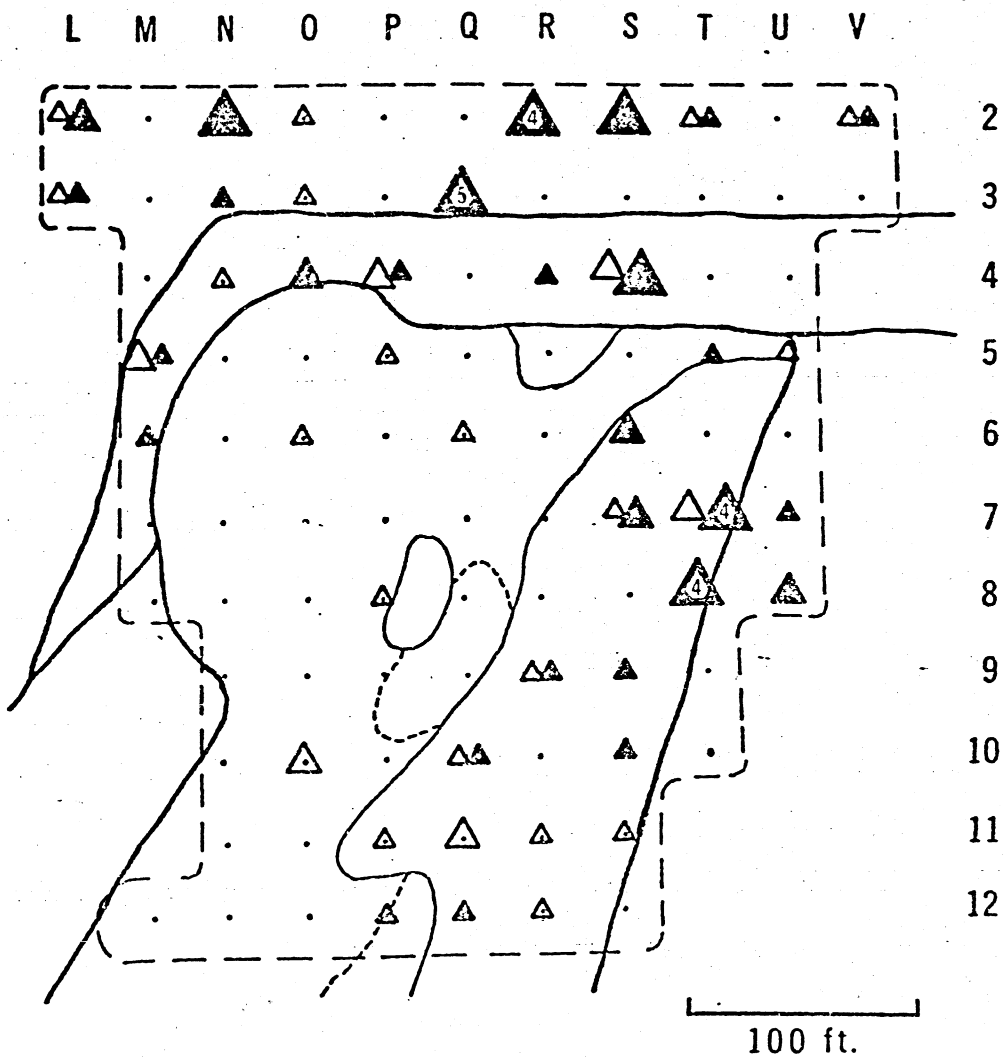

L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12
100 ft.

Fig. 27. Distribution of <u>Blarina brevicauda</u> captures, June, 1966-March, 1968.

	1	2	3	4 or more indicated by numerals
Snow-free months (April-Nov.)	△	△		
Winter months (Jan.-March)	▲	▲	▲	



L M N O P Q R S T U V
2
3
4
5
6
7
8
9
10
11
12
4
5
4
4
100 ft.

the summer than in the young aspen and red pine, where they were also frequently captured?

In order to shed some light on questions such as this and also to give a statistical measure of confidence to the analysis of distribution Table 4 was prepared. The latter table separates total captures by season, habitat, and species. Every trapping position in the study area was assigned to the appropriate habitat. In those few borderline cases in which a trapping position did not definitely lie in one habitat I assigned it arbitrarily to what I considered the more appropriate habitat. The total number of trap periods for each habitat was then calculated for each of the two seasons under consideration (snow cover present and snow-free). Trap periods include only those periods when a trap was felt to be operative, i.e. a trap period was not counted when a trap was knocked over by a raccoon, occupied by a chipmunk, or otherwise disturbed. The expected numbers of captures were calculated by multiplying the total number of captures of a species by the fraction representing the relative trapping effort for that habitat during that season. For example, there were 44 meadow mouse captures during the winter months. During the winter months 1358 of the 5257 trap periods were in the mature aspen. Therefore the expected number of meadow mouse captures in the mature aspen during the winter month is $44 \times \frac{1358}{5257}$, or 11.4 captures. Chi-square values were calculated for each season and for the total of both seasons. The column labeled Total Meadow is a sum of the <u>Poa</u> and <u>Bromus</u> columns and is not part of the chi-square calculations. The Yates correction for continuity was

Table 4. Distribution of captures of _Microtus pennsylvanicus_ (M), _Clethrionomys gapperi_ (C), _Peromyscus_ sp. (P), and _Blarina brevicauda_ (B) by habitat and season. Numbers in parentheses represent total trap periods for the respective seasons and habitats. The numbers to the left are actual captures and the numbers to the right are expected captures. See text for further details.

Season		Mature aspen		Young aspen		Red pine		Poa Phleum-Carex		Bromus		Total meadow		Total Cap.	χ^2
Winter (Jan.-Mar.) 1966, 1967, 1968		(1358)		(493)		(237)		(1977)		(1192)		(3169)		(5257)	
		cap.	exp.	cap.	exp.	cap.	exp.	cap.	exp.	cap.	exp.	cap.	exp.		
	M	1	11.4	-	4.1	-	2.0	17	16.5	22	10.0	43	26.5	44	37.0
	C	20	6.2	4	2.3	-	1.1	-	9.0	-	5.4	-	14.5	24	42.1
	P	-	.3	-	.1	-	.0	1	.4	-	.2	1	16	1	1.7 N.S
	B	22	13.7	9	5.0	3	2.4	1	19.9	18	12.0	19	31.9	53	26.5
Summer (April-Nov.) 1965, 1966, 1967		(1194)		(645)		(394)		(2106)		(1192)		(3298)		(5531)	
	M	-	115.3	23	62.3	25	38.0	298	203.3	188	115.1	486	318.4	534	234.8
	C	31	7.8	4	4.2	-	2.6	1	13.7	-	7.8	1	21.5	36	85.8
	P	32	8.2	4	4.4	1	2.7	1	14.5	-	8.2	1	22.7	38	6.1 N.S
	B	9	7.6	7	4.1	-	2.5	8	13.3	11	7.5	19	20.9	35	
Total		(2552)		(1138)		(631)		(4083)		(2384)		(6467)		(10,788)	
	M	1	136.7	23	61.0	25	33.8	315	218.8	214	127.7	529	346.5	578	261.3
	C	51	12.1	8	6.3	-	3.5	1	22.7	-	13.3	1	36.0	60	157.3
	P	32	9.2	4	4.1	1	2.3	2	14.8	-	8.6	2	23.4	39	71.9
	B	31	20.8	16	9.3	3	5.1	9	33.3	29	19.4	38	52.8	88	33.2

used in all chi-square calculations throughout this analysis when any expected value was five or less or when there was only one degree of freedom (Steel and Torrie, 1960, p. 357).

With the exception of Peromyscus during the winter and Blarina during the snow-free season all chi-square values are significant at the .001 level. Only one deer mouse was captured during all winter trapping. The distribution of the 35 short-tail shrew captures during the snow-free season was not significantly different from a random distribution. With these exceptions then, the species under consideration were not distributed randomly throughout the five habitats considered.

The basic distribution data, as presented in Table 4, will now be analyzed by species, for distribution within the habitats that were used, and also for change in distribution between seasons.

Microtus pennsylvanicus

Figures 19, 24, and Table 4 indicate that meadow mice were absent from the mature aspen during both seasons, and were confined to the meadow during the winter season. A considerable number of captures were made in the young aspen and red pine habitats during the snow-free season, however. In Table 5 only those habitats are considered where meadow mice were captured during the snow-free season. The chi-square value obtained is significant at the .001 level and indicates that even though meadow mice use the young aspen and red pine habitats during the snow-free season they are more heavily concentrated in the meadow.

Table 5. Summer distribution of *Microtus pennsylvanicus* captures.

Total meadow (3298)		Young aspen (645)		Red pine (394)		Totals (4292)	X^2
captures	expected	captures	expected	captures	expected	captures	
486	410.3	23	80.3	25	49.0	534	66.57***

In Table 6, only captures in the meadow are considered. The between habitat chi-square value for the snow-free season indicates that the distribution of captures between the two main areas of the meadow is not significantly different from a random one. On the other hand the chi-square value for the winter season is significant at the .01 level, indicating that meadow mice are more heavily concentrated in the *Bromus* portion of the meadow during the winter season.

Table 6 also presents an analysis of capture distribution between seasons for each of the meadow habitats. It is obvious that the raw data could not be used for this analysis due to the large difference in total numbers of captures between seasons. Therefore the snow-free season totals were adjusted so that these totals equaled the winter total, i.e., the snow-free season totals were multiplied by 43/486. Chi-square values calculated from these adjusted totals are not significant.

It appears, therefore, that meadow mice are found in the meadow, young aspen, and red pine in the snow-free months, but are most heavily concentrated in the meadow, and that in the winter meadow mice are found only in the meadow and primarily in one part of the meadow. This restriction of the area where meadow mice were trapped could be the result of either of two possibilities; (1) meadow mice move into the favored area during the winter, or (2) meadow mice living in the favored area survive and those in the other habitats do not. During the course of the study 15 meadow mice were trapped during both a snow-free season and a winter season. The distribution of captures of these

Table 6. Distribution of captures of *Microtus pennsylvanicus* in the *Poa* and *Bromus* portions of the meadow by season.

		Poa-Phleum-Carex	*Bromus*	Totals	X^2
Winter	cap./exp.	(1977) cap./exp. 17/26.8 17/20.8	(1192) cap./exp. 26/16.2 26/21.5	(3169) cap. 43	8.63**
Summer	cap./exp.	(2106) 298/310.3 26(adj.)/22.2	(1192) 188/175.7 17(adj.)/21.5	(3298) 486	1.63ns
Totals	cap.	(4083) 315	(2384) 214	(6467) 529	
X^2		1.01ns	1.49ns		

animals is presented by individual animals in Appendix A. The winter capture site of each animal was near the summer capture site of that animal. No meadow mice were captured in the winter that had been captured in the young aspen or red pine during the previous snow-free season. It appears, therefore, that the meadow mice which survive through the fall and early winter are animals already living in the meadow. The individual records in Appendix A also show no indication of movement from the *Poa-Phleum-Carex* portion of the meadow to the *Bromus* portion.

Clethrionomys gapperi

Figures 16, 25 and Table 4 indicate that red-backed voles are present in both the mature and young aspen habitats, and only in these habitats, during both seasons. Table 7 is an analysis of red-backed vole captures in these habitats. The winter distribution of captures between these habitats is not significantly different from a random one. The chi-square value based on the summer distribution of captures, however, is significant at the .01 level, indicating that during this season red-backed voles are more concentrated in the mature aspen.

When total captures between seasons are adjusted to a common level (as in Table 6) the calculated chi-square values indicate no significant difference in number of captures between seasons within habitats.

Only two red-backed voles were captured during both seasons. The capture distribution of each of these animals was a small area and showed no evidence of movement between seasons (Appendix B).

Table 7. Distribution of captures of <u>Clethrionomys gapperi</u> in the mature aspen and young aspen by season.

		Mature aspen	Young aspen	Totals	X^2
Winter	cap./exp.	(1358) cap./exp. 20/17.6 20/21.8	(493) cap./exp. 4/6.4 4/3.0	(1851) cap. 24	.76ns
Summer	cap./exp.	(1194) 31/22.7 21(adj.)/19.2	(645) 4/12.3 3(adj.)/4.0	(1839) 35	7.59**
Totals	cap.	(2552) 51	(1138) 8	(3690) 59	
X^2		.17ns	.13ns		

Peromyscus sp.

Figures 16, 26 and Table 4 indicate that, with the exception of one capture at the edge of the meadow, no deer mice were captured in the meadow during the 3298 summer trap periods in that habitat. Table 8 is an analysis of the summer distribution of deer mice captures in the remaining habitats. The chi-square value is significant at the .001 level, indicating that deer mice captures were concentrated in the mature aspen.

Only one winter capture of a deer mouse was made during the entire study. This animal was an adult female which had not been captured previously and was not captured again.

Blarina brevicauda

Figures 17, 27 and Table 4 indicate that short-tailed shrews were caught in all habitats. The summer distribution of captures of short-tailed shrews was the only distribution considered in Table 4 which did not differ significantly from an equal distribution across the five habitats.

The winter distribution of captures was significantly different from an equal distribution at the .001 level (Table 4). It is obvious, however, that most of the large chi-square value is a result of the large discrepancy between captures and expected captures in the *Poa-Phleum-Carex* habitat. In Table 9 this habitat is removed from consideration and the remaining habitats are analysed for winter distribution. The distribution across the remaining habitats is extremely close to that expected if there were equal distribution.

Table 8. Summer distribution of *Peromyscus* sp. captures by habitat.

Mature aspen	Young aspen	Red pine	Totals	X^2
(1194)	(645)	(394)	(2233)	
captures/expected	captures/expected	captures/expected		
32/19.8	4/10.7	1/6.5	37	16.42***

Table 9. Winter distribution of *Blarina brevicauda* captures by habitat.

Mature aspen	Young aspen	Red pine	*Bromus*	Totals	X^2
(1358)	(493)	(237)	(1192)	(3280)	
cap./exp.	cap./exp.	cap./exp.	cap./exp.		
22/21.5	9/7.8	3/3.8	18/18.9	52	.086

The distribution of captures of three short-tailed shrews which were captured a number of times in the winter are presented in Appendix C. One of these animals (No. 30) was captured in all four of the habitats where other short-tailed shrews were captured in the winter, one (No. 27) was captured in three of these habitats, and one (No. 24) was captured in two. These animals apparently moved freely and quickly within the area where they were trapped. Numbers 27 and 30 were both caught at opposite ends of their range within periods of 5 days. It appears, therefore, that the lack of captures in the _Poa-Phleum-Carex_ habitat is an avoidance of this area by otherwise widely ranging individual shrews.

Discussion

Microtus pennsylvanicus

In the course of this study, during the snow-free months, meadow mice were found in each of the habitats except the mature aspen. The mature aspen is the only habitat lacking a graminoid layer. During a trapping study (of 8 kinds of woods) in northern Michigan, Manville (1949) trapped meadow mice only in a northern white cedar swamp. Getz (1961a) found that in southern Michigan meadow mice occurred only in grassland vegetation where the plants were predominately graminoids. He also said that there was avoidance of meadow mice of areas containing only forbs and of grassy areas containing woody plants. On successional stages of abandoned farmland in Michigan, Beckwith (1954) found meadow mice in the highest concentrations in the "grass and other perennials" and the "mixed herbaceous perennials" successional stages. In a study of the distribution of small mammals throughout all of the habitats included in the prairie-forest transition in Minnesota and North Dakota, Iverson, et al (1967) found meadow mice only in grassland areas, smaller aspen groves, and aspen groves with a dense understory. In a study of food preferences of meadow mice, carried out at Itasca State Park, Thompson (1965) found that plant species characteristic of old-field habitats were far more acceptable to meadow mice than plants from tall-grass prairie, glacial marsh, boreal forest, or northern bogs. Four of the most characteristic and abundant species of the grass layer of my study area, *Poa pratensis*, *Phleum pratense*, *Bromus inermis*, and *Agropyron repens*, were in the top 10 preferred foods of the 30 tested by Thompson.

Although meadow mice were trapped in the young aspen and red pine habitats during the snow-free months they were concentrated in the meadow. There is a grassy understory in both the red pine and the young aspen but this layer is not as thick as in the meadow. Blair (1940) found larger populations of meadow mice in heavy cover of *Poa pratensis* and *Poa compress* than in sparse cover, and Eadie (1953) found significantly higher populations of meadow mice in a heavy cover of *Phleum pratense* than in a lighter cover. Lo Bue and Darnell (1959) found the density of *Microtus* populations positively correlated with vegetative height and cover in an alfalfa field.

Another possible explanation for lower concentrations of meadow mice in the red pine and young aspen is competitive exclusion by other species. Although Gottschang (1965) trapped *Microtus pennsylvanicus* and *Microtus ochrogaster* in equal numbers in the same field, others have found evidence of mutual exclusion between *M. pennsylvanicus* and other species of *Microtus*. Findley (1954), Getz (1962), Zimmerman (1965), and Lewin (1968) indicate that *M. pennsylvanicus* and *M. ochrogaster* are found in both moist, marshy areas and drier upland areas when only one species is present, but when both are present in a region *M. pennsylvanicus* is found in the marshy areas and *M. ochrogaster* in the drier areas. Findley (ibid) and Koplin and Hoffman (1968) found the same situation existing between *M. pennsylvanicus* and *M. montanus*.

In the present study the most closely related species to the meadow mouse is the red-backed vole. In an article reviewing the evidence for competitive exclusion between the genera *Microtus* and *Clethrionomys*, Cameron (1964) points out that on the coastal islands of Great Britain some islands are inhabited by *Microtus* and some islands are inhabited by *Clethrionomys*, but on none of the islands do they occur together. He further states that on ecologically diversified islands in North America where *Clethrionomys* is absent, such as Newfoundland, the Magdalen Islands, and Bonaventure Island, *Microtus* uses the habitat normally occupied by *Clethrionomys* (woodland) as well as the grassland areas. Clough (1964) introduced red-backed voles on two peninsulas in Nova Scotia where only meadow mice were present and four months later only meadow mice were captured on one peninsula and only red-backed voles on the other. In the aspen parkland of Saskatchewan, Morris (1969) found meadow mice restricted to the grassland and red-backed voles restricted to the aspen during the summer. In November, however, he found approximately equal numbers of each species within the aspen stands and numbers of meadow mice in adjacent grassland lower than in the aspen. He suggests that the greater snow depth in the aspen (due to drifting) has a survival value for both species which reduces competitive interaction. Both Cameron (ibid) and Morris (ibid) feel that the meadow mouse is excluded from woodland by the red-backed vole and not because it cannot adapt to the woodland.

Two lines of evidence from the present study indicate that interactions between meadow mice and red-backed voles may have partially restricted the habitats of both species. First, during the first summer of the study (1965) when red-backed voles were common in the mature aspen, neither species was trapped in the young aspen or red pine. No red-backed voles were captured during the second summer and comparatively few during the third, and meadow mice were captured in the young aspen and red pine those summers. Meadow mice did not invade the mature aspen during the second summer when no red-backed voles were captured. Secondly, the numbers of red-backed voles captured in the mature aspen were not significantly different from the numbers captured in the young aspen during the winter months, when meadow mice were trapped only in the meadow. In the summer months, when meadow mice were captured in the young aspen, red-backed voles were concentrated in the mature aspen.

Meadow mice and the woodland species of *Peromyscus* are generally not considered to be competitors. Wirtz and Pearson (1960) in studies of aggressive tendencies between *M. pennsylvanicus* and *P. leucopus* found that meadow mice were more aggressive than deer mice and may exclude deer mice from some old field habitats in New Jersey. However, Getz (1961a) mentioned that during the winter *P. leucopus* moved into a marsh occupied by meadow mice. In the present study there were only 6 captures of deer mice outside of the mature aspen during 3 summers of trapping and there was only one winter capture of a deer mouse.

The effect of short-tailed shrew predation on the distribution and abundance of meadow mice has been of interest to mammalogists since Plummer (1844) fed mice to captive shrews (and described their destruction). In a series of articles Eadie (1944, 1948, 1952) reviewed the literature of the previous 100 years and reported his own work. The literature indicates that short-tailed shrews are capable of preying on voles in nature. On the basis of meadow mouse remains in Blarina scats Eadie concluded that meadow mice formed a significant portion of the fall and winter diet of Blarina. Eadie did not, however, say anything about the effect of short-tailed shrews on the distribution of meadow mice. Getz (1961a) said that shrew predation was not an important factor in local distribution of meadow mice and conversely Getz (1961b) said that predation on meadow mice did not seem to influence the distribution of short-tailed shrews. Barbehenn (1958) found the two species to be randomly distributed with respect to each other in a uniform habitat. He also said that meadow mice shifted habitat preference at one time from an area avoided by short-tailed shrews to an area favored by them. Barbehenn concluded that "The presence of Blarina is more acceptable to Microtus than is a severe inanimate environment".

The data from the present study also strongly indicate that short-tailed shrews have little, if any, effect on the distribution of meadow mice. While Microtus were excluded from the mature aspen and definitely concentrated in the meadow portion of the remaining habitats during the summer months, Blarina were equally distributed across all habitats during these months. In the winter, short-tailed shrews were distributed equally in all habitats except they avoided the Poa-Phleum-Carex side of the meadow. This side of the meadow was also avoided by meadow mice during the winter months. It appears therefore that Barbehenn's statement quoted above is equally true in the winter months when all available habitats are under a heavy snow cover.

Meadow mice were only captured in the meadow during the winter months and were captured primarily within the Bromus side of the meadow. Two factors which might affect the winter distribution of Microtus are snow depth, and height and thickness of the grass cover. Formozov (1946, pp. 11-112) said that voles prefer to winter in places where snow is deposited by wind and avoid those places where the snow is blown away. He also said that shrews and voles mass in winter in coniferous forest clearings where the snow is deeper. Pruitt (1959a) noted that Clethrionomys rutilus appeared to avoid depressions in the snow caused by the limb cover of spruces, and that most mice used those areas of their home range where snow cover was thickest. Morris (1969) captured more meadow mice in aspen stands than in adjacent grassland in an area where snow cover is greater in the aspen stands due to drifting. I do not believe, however, that snow depth was a factor in small mammal distribution in the present study. The meadow was surrounded on 3 sides by forest and there was no evidence at any time of drifting. There was also no evidence of a difference in snow depth between the forest areas and the meadow. The only areas where there was less snow cover were the depressions directly under each red pine tree. In the areas between the pines the snow was as deep as in the other habitats. Getz (1961a) and Golley (1961) reported instances of meadow mice moving from areas of sparser grass-like vegetation to areas of heavier growth in early winter. Coulianos and Johnels (1962) mowed part of a timothy and clover field in the fall and found no sign of small mammal activity in this area the following spring. Many runways were found in the adjacent unmown areas. The latter authors feel that dense cover is attractive to small mammals in winter and that this may be due to the presence of a well developed subnivean air space in such areas. The *Bromus* side of the meadow had the heaviest grass cover in the present study area. It would, in fact, be difficult to find an area of vegetation anywhere which could produce such a uniform and high subnivean air space.

There was no evidence of movement into the meadow from the other habitats or into the *Bromus* area from the *Poa-Phleum-Carex* area. The evidence is rather that the animals caught in the winter in the *Bromus* area were the permanent summer residents of that area. The meadow mouse is a territorial species (Burt, 1940; Getz, 1961c) that is generally intolerant of other members of their own species (Getz, 1962). Van Vleck (1968) said that meadow mice outside their home range are forced to move on when confronted by a resident meadow mouse. The question which then remains is why do *Microtus* move into favored habitat in some cases (Getz, 1961a; Golley, 1961) and not in others (this study)? One possible explanation is that the winter movement and activity of the resident mice in the present study were not as restricted as populations in the other studies. Golley (ibid) found mice to be more restricted in their movements in winter than during the other seasons, Getz (1961c) found that mice remained very close to their burrows and nests in the winter, and estimated that their ranges were less than the area sampled by a single trap. Resident animals remaining very close to their nests should have comparatively little influence on incoming animals. Contrary to the previous reports the present study mice did not appear to be restricted in their movement. One mouse, for example, was trapped 105 feet away from where it had been captured 16 hours before during a period when the ambient air temperature reached a low of approximately -15° F. at the snow surface.

Although the thick Bromus habitat was the favored habitat for meadow mice in this study, the previously mentioned literature concerning the importance of snow depth suggests that this might not have been the case under other circumstances. If, for example, the same meadow and adjacent aspen forest were in an exposed situation where wind and drifting were important factors, the young aspen might be the favored habitat.

Clethrionomys gapperi

C. gapperi is a widespread species of woodland habitats. Manville (1949) trapped red-backed voles in all 8 types of woods sampled in northern Michigan, and Iverson, et al (1967) trapped this species in all habitats of the prairie-forest transition of Minnesota and North Dakota except the grassland areas. Butsch (1954) and Gunderson (1959) found that the highest concentrations of Clethrionomys were in areas with many rotting stumps and logs in moist or low areas. Butsch felt that the local distribution of the species was controlled by the availability of free water rather than suitable food. Odum had earlier (1944) demonstrated that red-backed voles consume a great deal more water per unit body weight than several species of *Peromyscus*, and had suggested that the high water requirement of *Clethrionomys* might be a limiting factor in its habitat selection. Getz (1968b) showed the water turnover rate in red-backed voles to be 2.2 times greater than in *P. leucopus* but calculated that the essentially nocturnal red-backed vole would lose only .02 grams of water a day more in a dry upland wood than in a low swamp. On this basis Getz feels that micro-climate is less important in the local distribution of the species than the availability of water, either as free water or in succulent food items.

In the present study red-backed voles were only captured in the mature and young aspen but were concentrated in the mature aspen during the summer months. The mature aspen was the wettest of the habitats and was the only habitat where stumps and fallen logs were present.

During the winter months *Clethrionomys* were apparently distributed evenly between the young and mature aspen. It has already been suggested that this could be due to the winter reduction of the habitats utilized by meadow mice. It is also possible that under a thick snow cover, with its uniform temperature and humidity, the mature aspen loses its advantage as a habitat. In the winter there is also a much more extensive and better developed subnivean air space in the young aspen, with its grass understory, than in the mature aspen. Beer (1961) said that red-backed voles centered their activity in a group of small brush piles during a period in which there was a light but continuous snow cover. In the present study there was no indication of movement from the mature to the young aspen. The latter observation is in agreement with the observation of Butsch (1954) that, although there was a reduction in size of individual home range following snowfall, there were no centers of concentration formed.

Red-backed voles occupied the same habitats with deer mice in this study. Red-backed voles are often found in the same habitat with _P. leucopus_ and neither species appears to influence the distribution of the other. Calhoun (1963) pointed out that even in regions where one species is dominant over the other the two species are still sympatric. In this case he assumed territorial avoidance to be operating to prevent the exclusion of the subordinate species. Getz (1968b) saw no evidence of either species being dominant over the other.

Peromyscus sp.

There were only 7 captures of deer mice outside of the mature aspen during the entire study. The woodland species of _Peromyscus_ are known to be widespread in various types of woods during the summer months. Manville (1949) captured _P. maniculatus gracilis_ in all of 8 types of woodland areas trapped. Iverson, et al (1967) found _P. leucopus_ in all forest types across the prairie-forest ecotone of Minnesota and North Dakota except very small aspen groves with a ground cover of grass. Getz (1961d) captured _P. leucopus_ in wooded areas which did not have a thick herbaceous layer.

Johnson (1926) captured P. leucopus equally in the interior of a wood and near the wood edge during both summer and winter, but the observations of a number of other workers have not supported his findings. Wood (1910) said that P. leucopus leave the thick woods in summer and are found along the forest edge and return to the thick woods in the winter. Nicholson (1941) found P. leucopus more frequently near the outer edge of woods during all seasons and noted that terrestrial nesting sites were used more commonly in the winter than in the summer. Weese (1924) also mentioned this autumn movement down to the forest floor but also said that there was an inward movement from the forest margin at that time. Gottschang (1965) said that P. leucopus were frequently trapped in the tall grass around the edges of fields during winter months and Getz (1961a) mentioned the winter movement of a number of P. leucopus into a marsh.

During the present study there was only one winter capture of a deer mouse during more than 5000 trap periods. Fuller, et al (1969) found a similar situation in northern Canada where, "Peromyscus are almost impossible to trap during winter". They feel that this is explained by the discovery that P. maniculatus undergo frequent, prolonged periods of torpor even when caged alone and supplied with food in excess (Stebbins, 1968). Howard (1951) had previously observed that P. maniculatus entered torpor when allowed to huddle in groups, and Morhardt and Hudson (1966) induced torpor in this species by food deprivation. Fuller, et al (ibid) suggest that the seeds and berries used by deer mice are difficult to find in the snow and torpor becomes an advantage.

They feel that the poorer survival of deer mice, in their study, after a mild winter could be due to the mice spending less time in torpor hence increasing their energy demands.

Another possible explanation for the lack of winter captures is that the deer mice form widely scattered aggregations during the winter. Thomsen (1945), working in central Wisconsin, found *P. leucopus* living in widely separated groups, of from 3 to 6 animals, during the winter months. Thomsen said that individuals did not range farther than 30 feet from the group shelter. Nicholson (1941) also said that *P. leucopus* live together in the winter in small groups and that these aggregations begin to break up in March with the onset of breeding.

Torpor and winter aggregation are not mutually exclusive, of course. Deer mice could aggregate and then enter torpor. In the present study if aggregates formed none were within range of the traps in the relatively small area trapped in the woodlot. Even if the deer mice did enter torpor to some degree it appears unlikely that they would not be trapped occasionally if they overwintered within the study area. It may also be pertinent that the single winter deer mouse capture occurred on March 16, when the aggregations should be breaking up. On that night the temperature was -27° F. at snow top level and there were tracks on the newly fallen snow next to the chimney where the animal was caught. It appears, therefore, that temperature alone was insufficient to induce or hold torpor in this *Peromyscus*.

Blarina brevicauda

In an early laboratory study of the effect of air conditions on mammalian distribution, Chenoweth (1917) determined that Peromyscus leucopus always moved to air of lowest evaporative power in a gradient cage. He said that the short hair of B. brevicauda would not protect them well from dry air conditions and were more restricted in habitat than P. leucopus, perhaps for this reason. Later workers have confirmed the importance of moisture but this has not proved to be a factor limiting distribution in most habitats. Pruitt (1953, 1959b) and Getz (1961b) found moisture to be of primary importance in the local distribution of Blarina but Pruitt (1959b) also determined that the air in an artificial shrew burrow remained saturated at soil moistures from 40 percent to 0. Jameson (1949) had also noted that the air in small mammal tunnels was usually saturated. Both Pruitt (1953) and Getz (ibid) failed to trap Blarina only in extremely dry habitats. Manville (1949) trapped short-tailed shrews in all 8 types of woods sampled and Jameson (ibid) found this species abundant in all 6 woodland areas trapped. Iverson, et al (1967) said that Blarina were common in all of the habitats of the prairie-forest ecotone of Minnesota and North Dakota, with the exception of riparian woodland. The literature relating to the species is consistent with the present study in which Blarina were equally distributed across all habitats during the summer months.

Short-tailed shrews were also distributed equally across all habitats in the winter with the one exception of the Poa-Phleum-

Carex side of the meadow. The fact that both Blarina and Microtus avoided that side of the meadow in the winter might suggest that the absence of Blarina is related to the absence of Microtus. The distribution of short-tailed shrews was not otherwise correlated with that of meadow mice or any other potential prey species during either season.

Pruitt (1959b) suggested that Blarina are limited to areas with stable soil temperature, sufficient moisture in the soil to saturate burrows, and a soil matrix that has enough litter to allow tunnels to remain intact. The first two factors are probably not significant in the present study. The insulating snow cover was equally thick on both sides of the meadow, and Bader, et al (1954) demonstrated that air within a snow mass is almost always saturated. The avoidance of the Poa-Phleum-Carex side of the meadow by both a herbivore (Microtus) and an insectivore (Blarina) appears to indicate that this side of the meadow was physically less attractive in the winter, perhaps due to a less well developed subnivean air space.

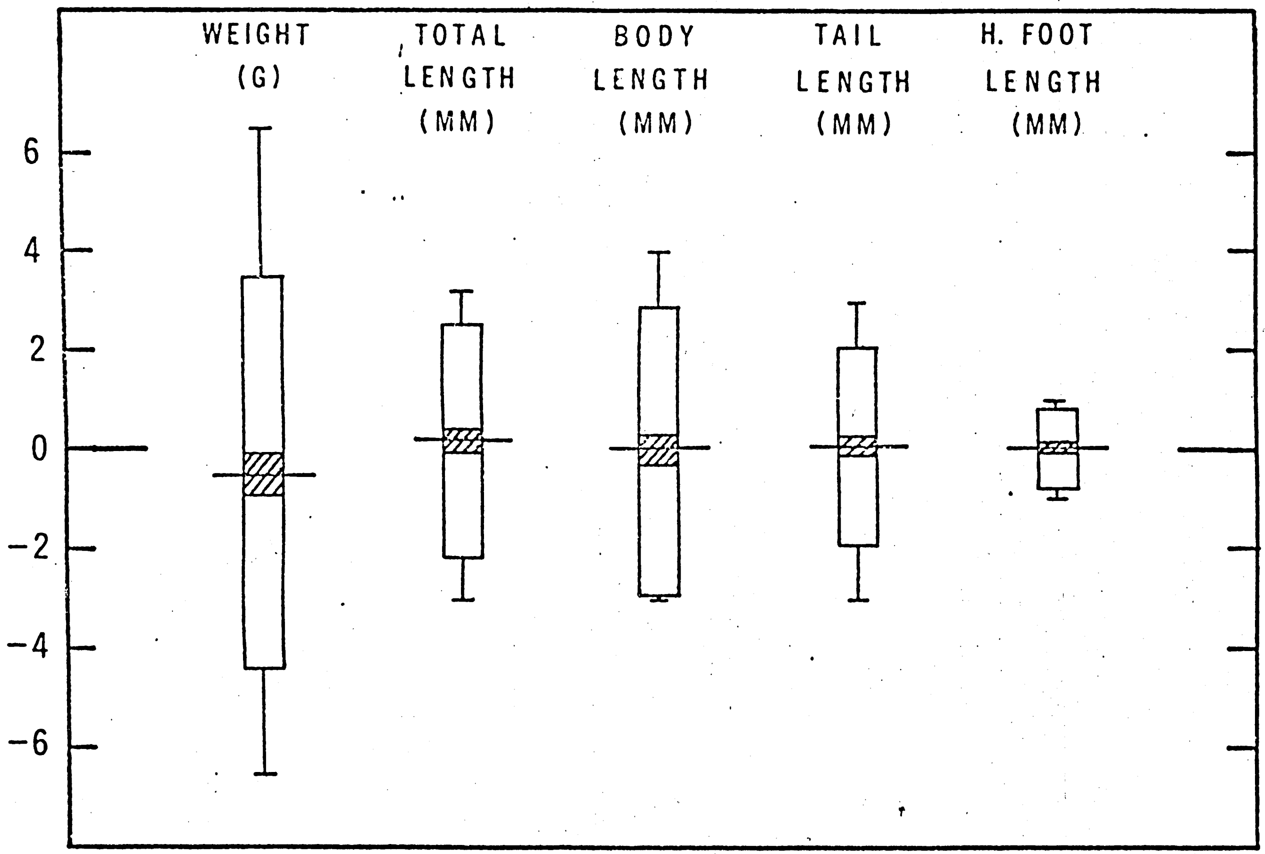
GROWTH

Reliability of measurements

There are very few studies of growth on individual small mammals in the field and in only one study of which I am aware were linear measurements as well as weight taken. Chew and Butterworth (1959) measured Kangaroo rats (Dipodomys merriami) in the field as well as in the laboratory but discontinued body length measurements after the animals were three-fourths grown because "the struggling of the animals made the results too unreliable". It is obviously necessary to determine the reliability of the measurements if these data are to be used meaningfully.

During the course of this study successive measurements within a 24 hour period were made on individual M. pennsylvanicus. Nine out of a total of 87 of these successive captures were less than 24 hours apart and the rest were approximately 24 hours apart. The difference between the first measurements and the successive measurements can be used as an indication of the reliability of field measurements and is shown in Figure 28. This is the only measurement of the reliability of weight and linear measurements that has been made on living small mammals. Figure 28 shows that weight varies within a large range ($\pm$ 6.5 grams) within a very short period of time. If weight losses due to parturition had been included the range would have been much larger. Five females trapped before and after parturition and within a three day period, showed weight losses of 8.5, 19.5, 11.0, 13.0, and 14.5

Fig. 28. Difference between successive measurements of *M. pennsylvanicus* within a 24 hour period (N=87). Symbols show mean, range, 95% confidence limits for individual measurements and 95% confidence limits for the mean.



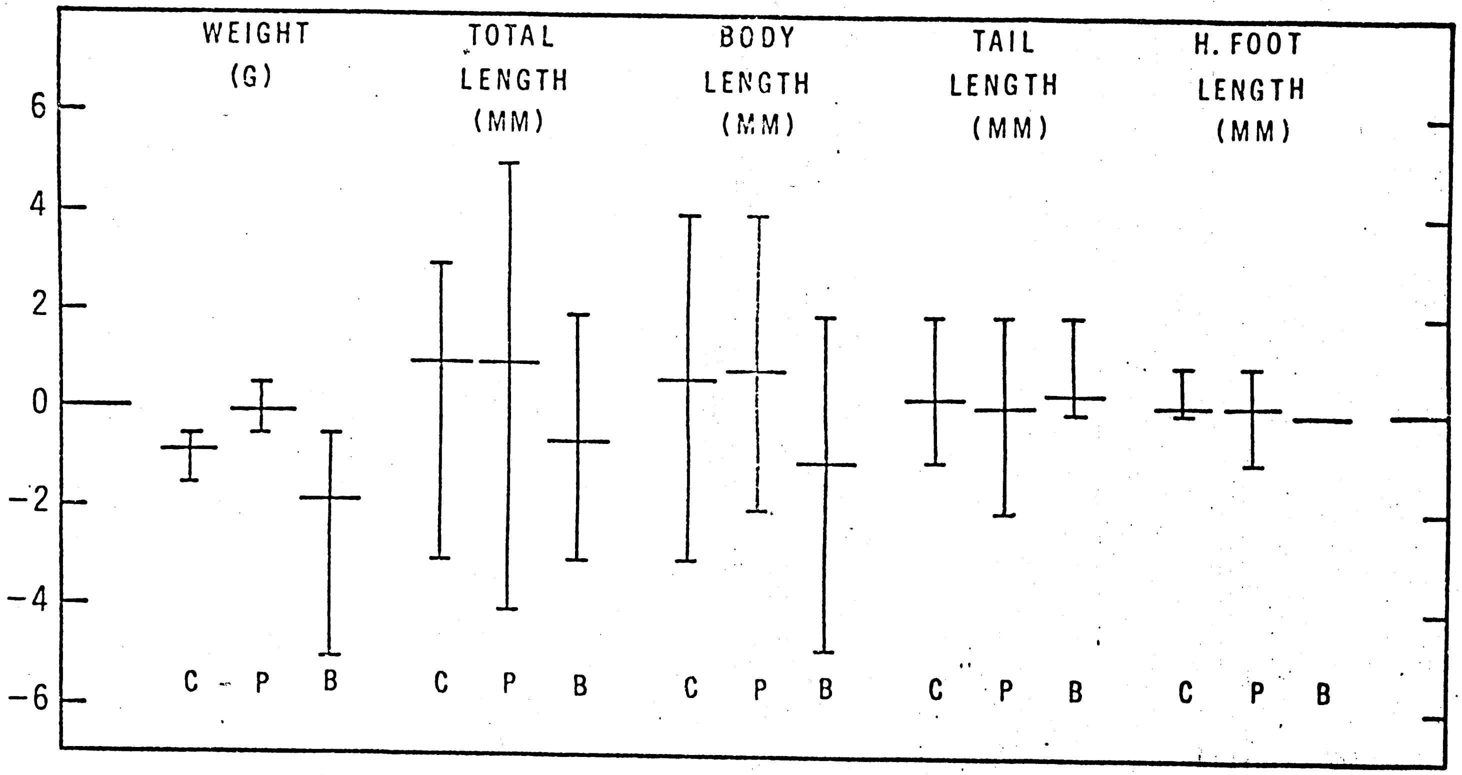
WEIGHT (G)
TOTAL LENGTH (MM)
BODY LENGTH (MM)
TAIL LENGTH (MM)
H. FOOT LENGTH (MM)
6
4
2
0
−2
−4
−6

grams. Barbehenn (1955) also mentioned large daily fluctuations of individual weights in M. pennsylvanicus, and said that weight losses of 15 to 20 percent of "normal" body weight,due to trap confinement, were not uncommon. In the present study one weight change resulted in representing a 22 percent change using the heavier weight as the "normal" weight, and a 28 percent change when lighter weight was used in the computation. Dawson (1967) said that the mechanics of weighing mice in the laboratory is accurate to within 0.4 percent. Although the mechanical accuracy of weights taken in the field is not this high, there is no doubt that the major cause of the very large fluctuations in weight shown in Figure 28 is biological.

Conversely, it can be assumed that very rapid changes do not occur in linear dimensions and that the differences between the successive linear measurements shown in Figure 28 are due to the mechanics of measurement. In his study of variability of growth in M. pennsylvanicus, Whitmoyer (1956) pointed out that "a great proportion of the variability observed in linear measurements may well be due to human error". The human error in the mechanics of measurement turns out to be much less than the biological variation in weight already mentioned. The largest percentage of difference for total length measurements was 2.1%. The largest percentage of difference for weights was more than ten times greater. The largest percentages of difference for body length, tail length, and hind foot length, were 3.6%, 9.1% and 6.3% respectively. The tail length measurement is the least accurate linear measurement probably because of the subjectivity in determining the location of the tail base. Errors in measurement of the tail influence directly body length measurement since the body length was determined by subtraction of tail length from total length. The percentage of error for body length is much smaller, however, because body length is more than three times the tail length. Data for measurement reliability analysis of the other small mammal species studied are not available. There were 6 successive captures of individual Clethrionomys gapperi within a 48 hour period, 6 successive captures of individual Peromyscus sp. within a 48 hour period, and 5 successive captures of individual adult Blarina brevicauda within a 7 day period. The ranges and means for the differences in these species are shown in Figure 29. Although this figure is based on a small number of measurements and a longer period of time between measurements, it suggests that weight may not be as variable for Peromyscus sp. and C. gapperi as for M. pennsylvanicus. The smallest changes in successive weights were recorded in Peromyscus sp. but even in this species the largest percentage difference in weight (5.9%) was larger than the largest percentage difference in total length (3.9%). The latter was the largest percentage difference in total length recorded in the entire study.

It is apparent therefore that linear measurements made on small life mammals are more reliable than weight measurements. The fact that most field studies of growth have used only body weight is perhaps largely because, as Forbes (1964) pointed out, "Unfortunately, the measurement most easily taken on a living small mammal is body weight".

Fig. 29. Difference between successive measurements of *C. gapperi* (C) and *Peromyscus* sp. (P) within a 48 hour period, and *B. brevicauda* (B) within a 7 day period.


WEIGHT (G)
TOTAL LENGTH (MM)
BODY LENGTH (MM)
TAIL LENGTH (MM)
H. FOOT LENGTH (MM)
6
4
2
0
-2
-4
-6
C P B
C P B
C P B
C P B
C P B

Microtus pennsylvanicus

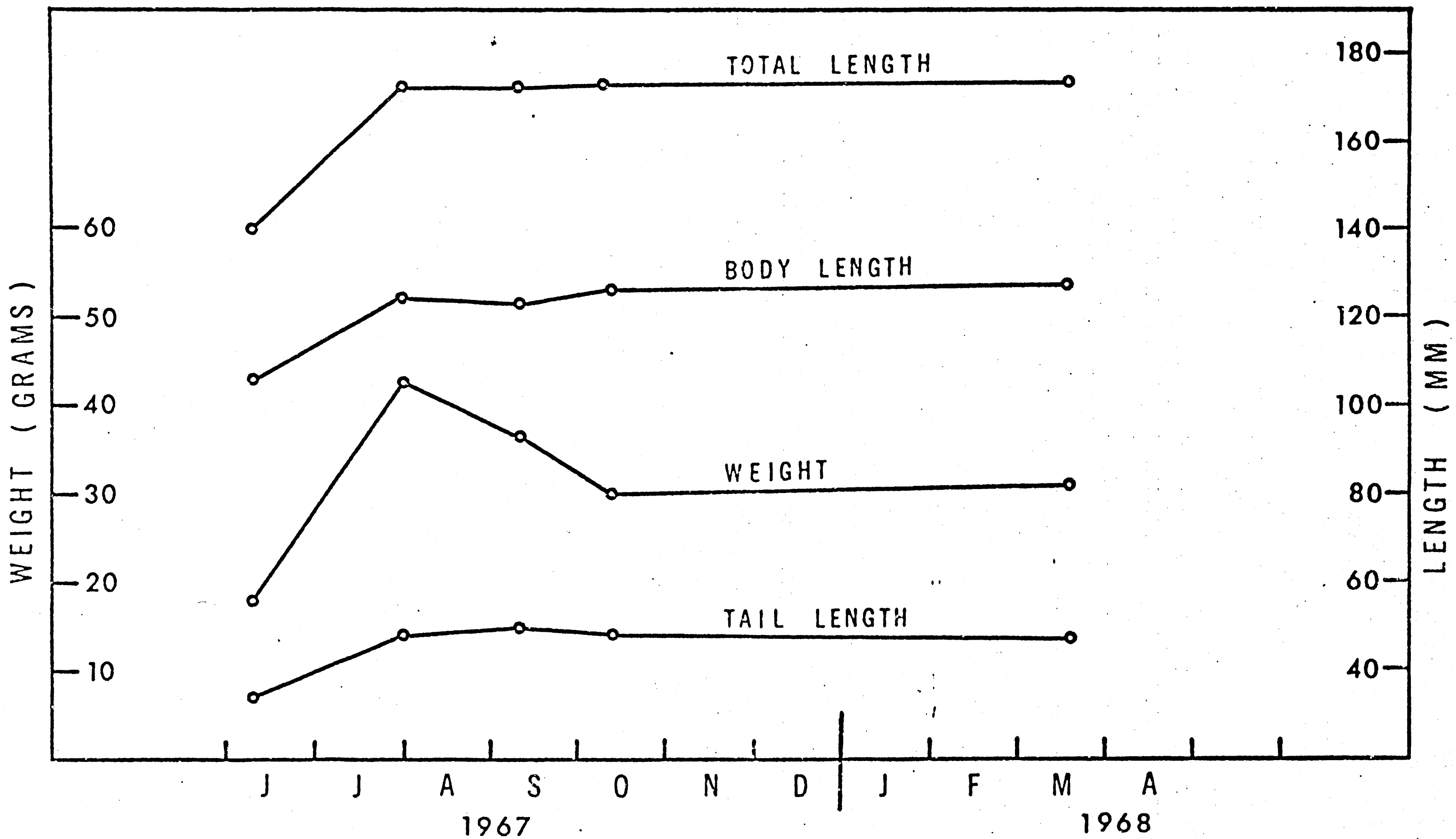
In all analysis of growth the first measurements taken on an animal during a session are used.

Figure 30 depicts the growth of an early summer juvenile Microtus (No. 172) for which there is fairly complete data. Figure 31 shows the growth of two very small juveniles and can be used to illustrate the two weeks of growth preceding the first capture of No. 172. The latter meadow mouse was born in early May and reached, in three months or less, as large a size as any meadow mouse taken in the study. A composite picture of growth for a M. pennsylvanicus born in early May is shown in Figure 32.

There are only two field studies of growth in M. pennsylvanicus (Hamilton, 1937b, 1941; Barbehenn, 1955) and both of these studies were conducted near Ithaca, New York. The growth of No. 172 (Fig. 30) agrees very well with Hamilton's study, in which mature weight was achieved in 12 weeks. Hamilton's mice were heavier than those in the present study, however. He took a number of males which weighed over 60 grams. In the present study only two mice (one male and one female) were taken which weighed over 50 grams.

Throughout the present study similar sized animals captured in the same season displayed increases in linear dimensions that were remarkably synchronous. Up to a weight of 18-20 grams weight increases were also synchronous, but above that weight the increases were variable. Barbehenn (1955) also mentioned large variation in growth rate (weight) in subadult and adult mice.

Fig. 30. M. pennsylvanicus No. 172 (female).



TOTAL LENGTH
BODY LENGTH
WEIGHT
TAIL LENGTH
WEIGHT (GRAMS)
60
50
40
30
20
10
LENGTH (MM)
180
160
140
120
100
80
60
40
J J A S O N D J F M A
1967
1968

Fig. 31. M. pennsylvanicus No. 112 (male, o—) and No. 113 (female, Δ--).

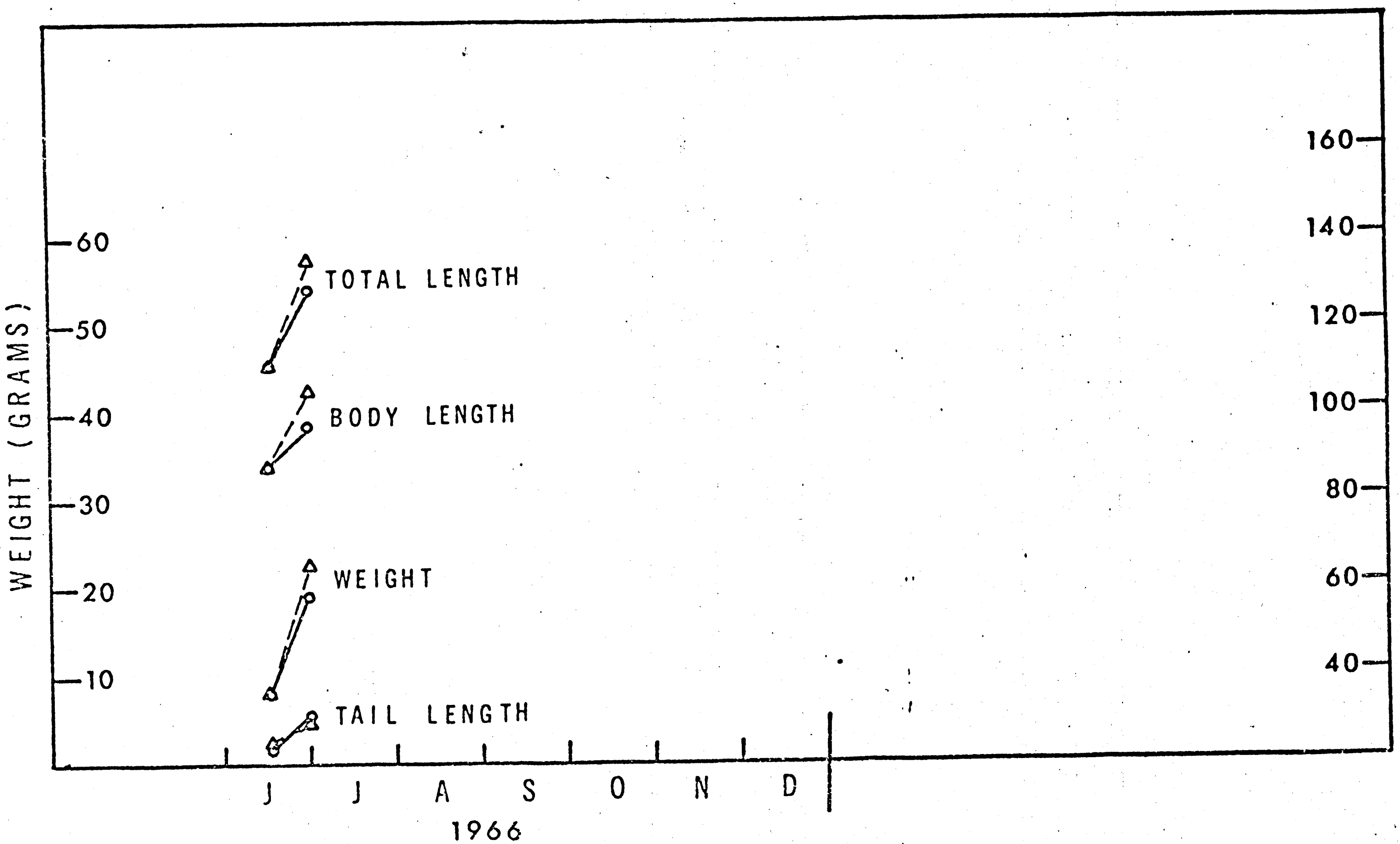
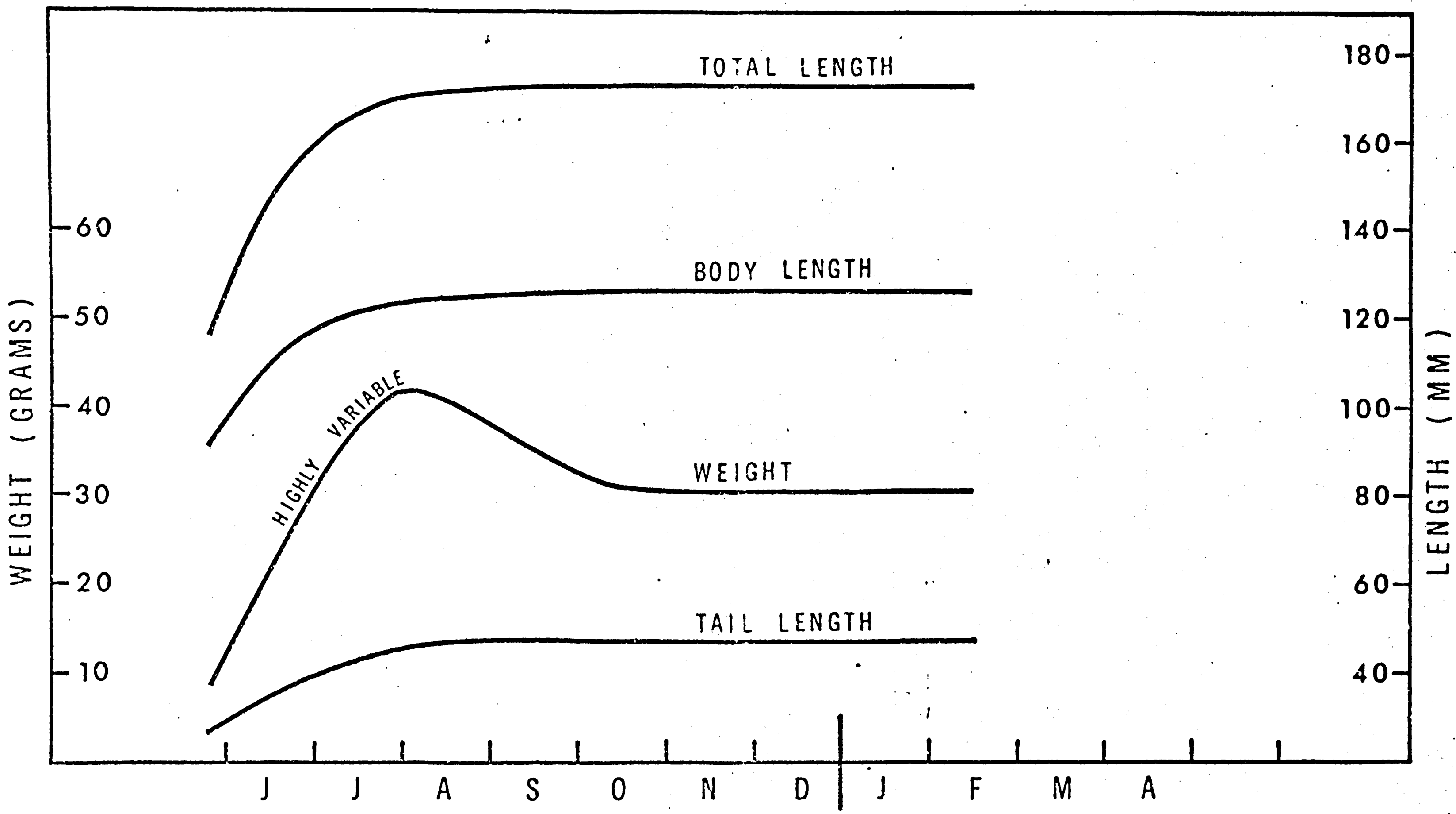

TOTAL LENGTH
BODY LENGTH
WEIGHT
TAIL LENGTH
WEIGHT (GRAMS)
60
50
40
30
20
10
LENGTH (MM)
160
140
120
100
80
60
40
J
J
A
S
O
N
D
1966

Fig. 32. Composite picture of growth for a M. pennsylvanicus born in early May.


TOTAL LENGTH
BODY LENGTH
WEIGHT
TAIL LENGTH
HIGHLY VARIABLE
WEIGHT (GRAMS)
LENGTH (MM)
10
20
30
40
50
60
40
60
80
100
120
140
160
180
J
J
A
S
O
N
D
J
F
M
A

During the first winter of the study (1966) the meadow mice captured were very similar in size. These mice were approximately 17 grams in weight and were 130-140 m.m. in total length with body length of 100-105 m.m. On the basis of any of these measurements these animals would be assumed to be young animals. On the basis of Hamilton's (1937b) growth curve, a body weight of 17 grams would be reached within 12 to 18 days. Whitmoyer's (1956) laboratory study of growth in *M. pennsylvanicus* indicates that a weight of 17 grams and a tail length of 30 m.m. would be reached in approximately 20 days. In the present study young mice in early summer reached the size of these winter mice in 30 days or less (Fig. 31). Three of the mice captured during the winter of 1966, however, had been captured as very young juveniles the previous summer (females 76, 84, 67). These animals were all born in mid-July and were therefore six months old in mid-January. The measurements of No. 76 and No. 84 are shown in Figure 33. Mouse No. 67 was first captured just prior to a change in technique in making the linear measurements and is therefore not shown.

The results of the following years confirmed the lack of growth in fall and winter. Figure 34 shows the results of measurements made on male *M. pennsylvanicus* No. 151. This animal was captured over a longer period of time than any other animal in the study. The results of measurements made on female *M. pennsylvanicus* No. 150 are also shown to illustrate the remarkable similarity of size attained by mice of the same age but different sex over a long period of time.

Fig. 33. *M. pennsylvanicus* No. 84 (female, o—) and No. 76 (female, Δ– –).

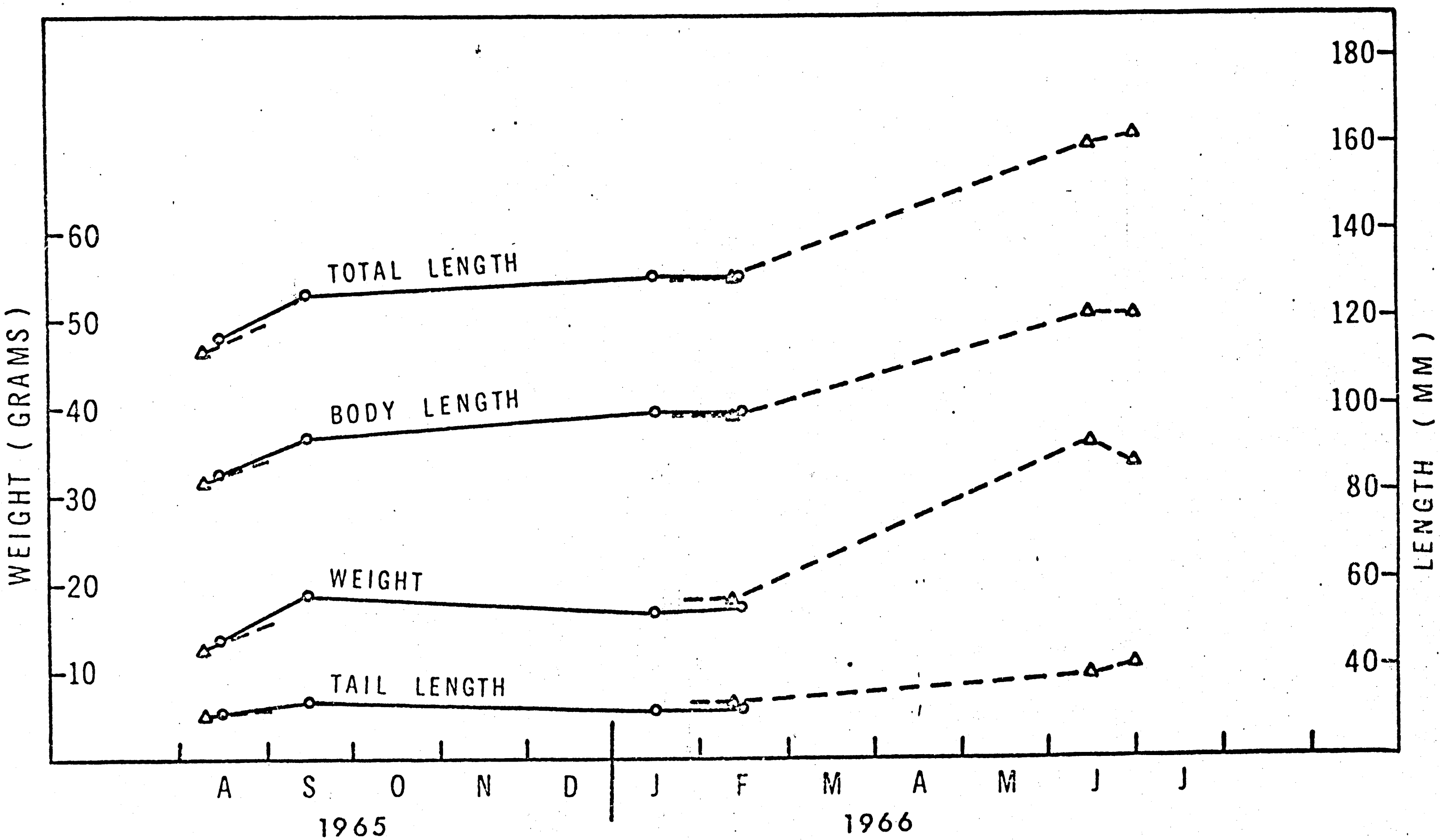
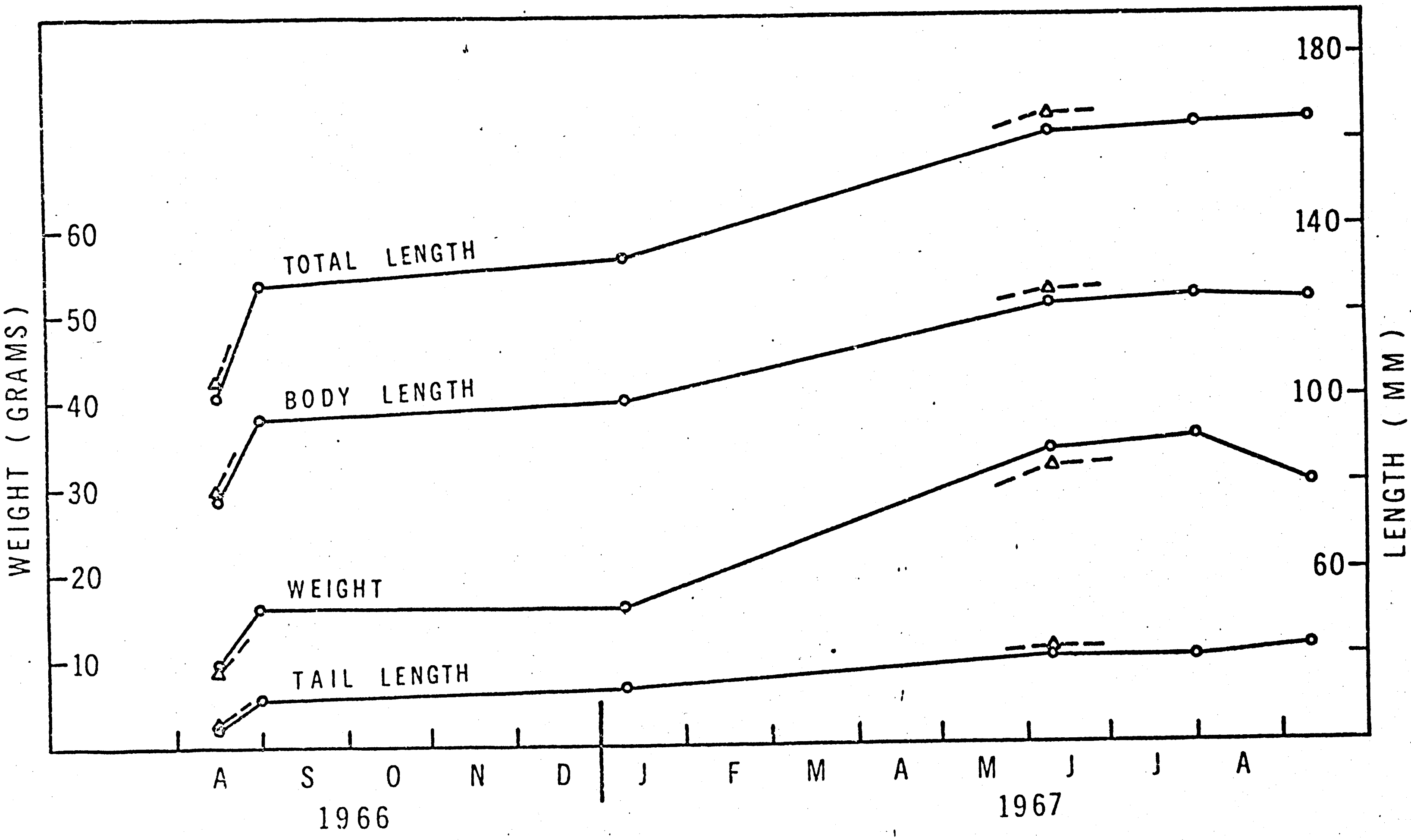

TOTAL LENGTH
BODY LENGTH
WEIGHT
TAIL LENGTH
WEIGHT (GRAMS)
LENGTH (MM)
60
50
40
30
20
10
180
160
140
120
100
80
60
40
A
S
O
N
D
J
F
M
A
M
J
J
1965
1966

Fig. 34. *M. pennsylvanicus* No. 151 (male, o—) and No. 150 (female, △--).

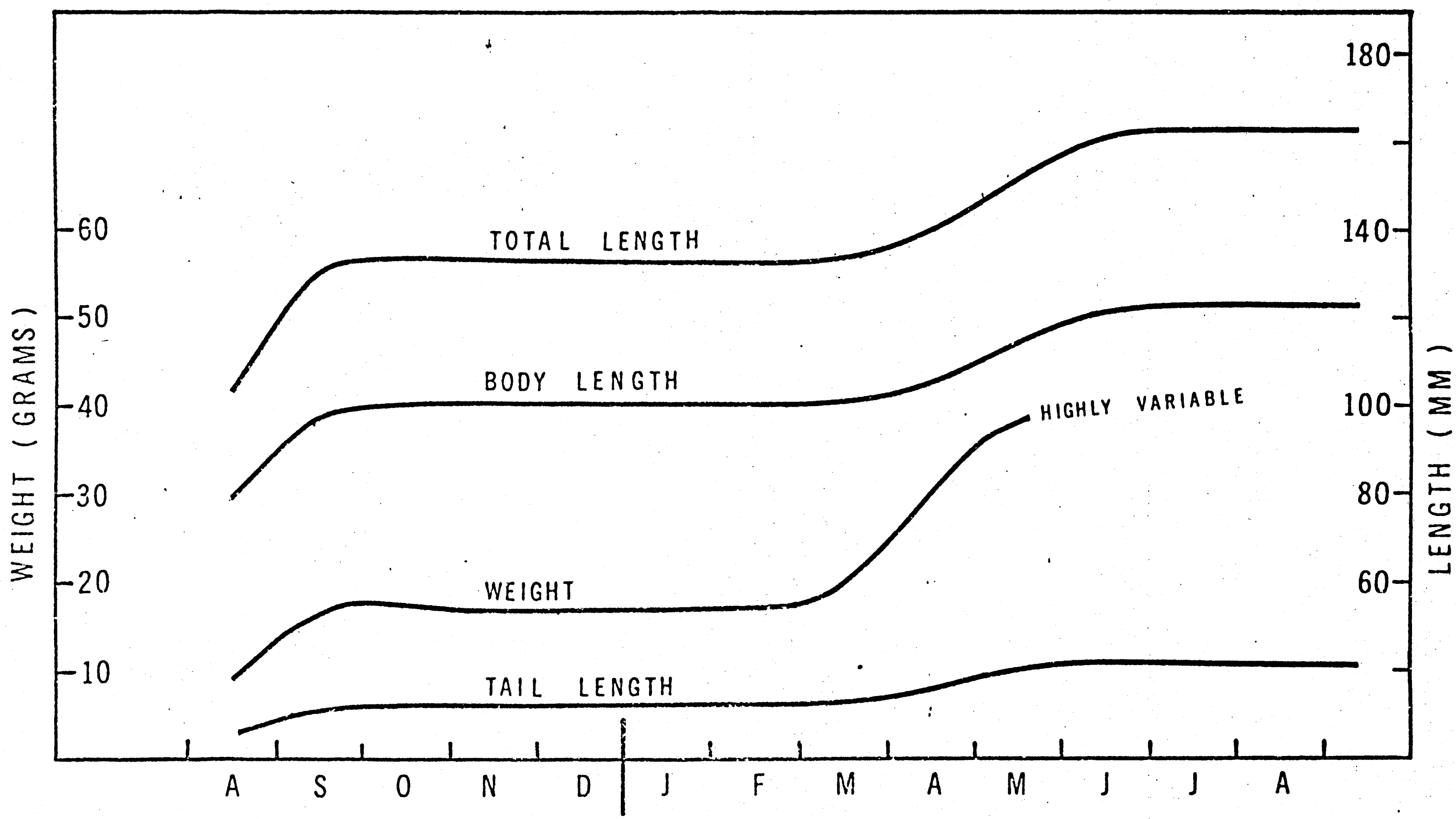


TOTAL LENGTH
BODY LENGTH
WEIGHT
TAIL LENGTH
WEIGHT (GRAMS)
10
20
30
40
50
60
LENGTH (MM)
60
100
140
180
A
S
O
N
D
J
F
M
A
M
J
J
A
1966
1967

The lines connecting the measurements in Figures 33 and 34 are drawn as straight lines. This does not give as accurate a picture of growth as that which can be obtained by using other available data to fill in the long periods between captures. For example, there was no evidence of spring linear growth by overwintering animals until some time after mid-March. One animal (No. 160) was measured in January, late April, and early June, and could be used to add a point between March and June. Several animals captured in mid-March were slightly heavier than in the previous winter, so it appears that spring growth in weight starts slightly ahead of linear growth. Weight also "overshoots" in the fall, slightly exceeding the weight maintained during the winter. After weight and linear growth have leveled off in the fall there is a complete lack of growth, within the accuracy limitations of the measuring system, until growth resumes in early spring. There is very little growth after early June in linear dimensions and what growth occurs is in body length. The composite picture of growth for a _M. pennsylvanicus_ born in early August is given in Figure 35.

This picture of growth is accurate for animals born between mid-July and early September. Male _M. pennsylvanicus_ No. 259 was captured as a 10.5 gram/115 m.m. juvenile on September 14, 1967 and was captured as a 16.5 gram/133 m.m. animal on October 13, 1967. This animal grew to the overwintering size achieved by the other late summer juveniles (Fig. 33, 34, 35) during a period of the year when no growth was recorded for any other _M. pennsylvanicus_ during the entire study. It appears therefore that a

Fig. 35. Composite picture of growth for a *M. pennsylvanicus* born in early August.


WEIGHT (GRAMS)
60
50
40
30
20
10
TOTAL LENGTH
BODY LENGTH
HIGHLY VARIABLE
WEIGHT
TAIL LENGTH
A
S
O
N
D
J
F
M
A
M
J
J
A
180
140
100
80
60
LENGTH (MM)

certain size must be reached before growth stops and that when this size is reached (for animals born after mid-July) growth stops.

Because No. 172 (Fig. 30) had become, by the beginning of August or earlier, as large in size as any meadow mouse trapped in the study, it is not possible to say in this case whether this was a seasonal stoppage of growth or simply a case of reaching a maximum size. An animal born approximately one month later (early June) stopped growing by the end of August at a length of 146 m.m. It appears then that meadow mice born after early or mid-May experience a seasonal stoppage of growth in the period from late August to mid-September.

All meadow mice displayed a loss of weight (Figs. 30, 32, 35) starting at the same time that linear growth ceased. Weight was less variable during the fall and winter months at the lower weight.

These results are of interest both in terms of growth theory and because weight and linear dimensions have been used extensively to age small mammals. On the basis of extensive museum collections August Dehnel published a paper (1949) in which he said that there were seasonal variations in the skulls of shrews of the genus Sorex. The latter paper stimulated further investigations in Professor Dehnel's laboratory in Poland and by a number of Russian scientists. Their work was reviewed by Pucek (1964) and by Schwarz, et al (1964). Growth rate, age of sexual maturation, and a number of other measurements in both shrews and rodents were shown to vary with time of birth. Bee and Hall (1956) said that seasonal generations of Clethrionomys rutilus, Microtus oeconomus, and M. miurus snap-trapped on the arctic slope of Alaska differed in skull proportions and that animals born in the spring were larger than those born during other seasons. Dapson (1968) argued that the changes in dimensions of an individual animal are not necessarily those shown by samples taken from the population during the course of the year. In his study of Blarina brevicauda he found that seasonal fluctuations in skull dimensions apparent at the population level did not exist at the individual level and were caused by differences in growth between spring and fall-born animals and their varying proportions in the population.

Hamilton (1937b) noted an almost complete lack of large M. pennsylvanicus during the winter months but said that there was little indication of weight reduction in individuals and the lack of large animals must be due to the death in the fall of the large animals. Chitty (1952) mentioned a winter loss of weight in M. agrestis, and Barbehenn (1955) reported a fall loss in weight of several male M. pennsylvanicus. Bergstedt (1965) found that growth in weight in Clethrionomys glareolus in Sweden ceased during the winter months. Sealander (1966) and Fuller, et al (1969) noted a winter weight loss in C. rutilus. The latter authors said that this decrease in body weight occurs in most, if not all, Holaractic microtines and is the result of 3 processes - death of the largest animals, cessation of growth in the youngest, and loss of weight in the older animals that survive. The present study demonstrated that M. pennsylvanicus lose weight in the fall and in addition demonstrates that meadow mice of all ages stop growing in linear dimensions in the fall as well.

The ability to determine the age of a mammal in hand is one of the most important and perplexing problems facing a field mammalogist. The problem is particularly difficult if the animal cannot be sacrificed. Tooth height has been used to age shrews (Pearson, 1945; Dapson, 1968) but is of no use in aging rodents and would be difficult to use on living shrews. Lens weight (e.g. Hoffmeister and Getz, 1968) and bone clearing and staining techniques (Harrington, 1955) are fairly accurate but are of no use in aging living animals.

Body weight has been the most widely used means for determining the age of M. pennsylvanicus in the field. The growth data of Hamilton (1937b, 1941) have been used by other workers (e.g. Cook and Beer, 1958; Golley, 1961) to estimate the ages of meadow mice throughout a yearly cycle. Barbehenn (1955) and Whitmoyer (1956) pointed out that body weight is a poor method of determining age in M. pennsylvanicus on the basis of large daily changes in weight and in large variability between individuals of the same known age. The present study demonstrated that age of M. pennsylvanicus could be misjudged by as much as 5 months, using weight as the criterion of age.

Linear dimensions were shown to be better than weight for age determination for two reasons. Linear measurements are more reliable, repeatable over a short period of time, and they do not decrease, as does weight. It is not possible in all cases to determine age with certainty, even with linear measurements. On the basis of indirect evidence, Barbehenn (1955) concluded that the heavier males seen after late June were the young of that spring. In the present study a late summer animal (Fig. 34) was smaller in linear dimensions the following summer than a spring born animal (Fig. 30). An animal born later in the spring or early summer can be exactly the same size as an animal born late the previous summer. Furthermore in the present study the mice captured during the third winter (1968) were larger and were born earlier than the mice seen the previous winters. It is obvious that any interpretation of age, even on the basis of linear measurements, is complex and variable.

The results of this study illustrate the possible dangers of using data from one season for interpretation of data from another. I also feel that data from one geographic area should be used with caution to interpret data from another area. It would be as invalid to use Figure 35, to interpret trapping results in New York, as it is to use Hamilton's (1937b) growth curve to interpret winter data.

Blarina brevicauda

The limited data of this study confirm the observation of Dapson (1968) that the long bones of this species grow little after the animal enters the trappable population. The smallest *B. brevicauda* (in linear dimensions) seen in this study was 118 m.m. in total length. The longest animal had a total length of 141 m.m. In contrast the smallest *M. pennsylvanicus* taken were only one half as long as the largest.

The short-tailed shrews captured in the winter were as large and heavy as the summer animals. The two animals captured in the summer and later captured in the winter were both heavier in the winter. This appears to indicate that the size of the winter animals is not merely an artifact of the survival of an older cohort. Dapson (1968) showed that the growth rate of *B. brevicauda* born in the summer was fairly constant regardless of season. Dapson said that the *Blarina* in his study had depleted their fat reserves by January but presented no quantitative measurements. The two observations made in the present study do not indicate a weight loss in the fall.

Clethrionomys gapperi and Peromyscus sp.

The data on these species are too limited for analysis.

ACTIVITY

Results and discussion

During the winter sessions traps were checked at regular 8 hour intervals (at 0800, 1600, and 2400). The number of captures during each period of the day can be used as a relative measure of activity. Traps were checked at the same 8 hour intervals during 4 snow-free trapping sessions to serve as a basis for comparisons of activity between winter season and snow-free season.

Microtus pennsylvanicus

Table 10 lists captures of meadow mice by period of the day. The distribution of captures during the winter trapping sessions differed significantly from a random distribution. It appears that the meadow mice were most active during the 1600-2400 period, and that they were least active during the 2400-0800 period. Prior to 1968 all winter trapping sessions started at 1600, but in 1968 one session started at 1600 and one session at 0800. The higher totals during the 0800-1600 period in 1968 raised the doubt that the number of captures during each period of the day might also be a function of the period of the day when each session started, i.e. were the animals trapped in greater numbers during the early periods of a session? In order to test this possibility captures which occurred during the first 6 periods of a session were arranged according to consecutive periods of the session. Table 11 presents this distribution of

Table 10. Distribution of *Microtus pennsylvanicus* captures by period of the day.

	2400-0800	0800-1600	1600-2400	X^2
A. Winter				
Jan.-Mar. 1966	1	2	7	
Jan.-Mar. 1967	1	2	8	
Jan.-Mar. 1968	3	10	7	
Totals	5	14	22	10.59**
B. Snow-free				
Aug. 30-Sept. 1, 1966	8	20	10	
Nov. 3-5, 1966	2	1	3	
Apr. 28-30, 1967	3	5	3	
Aug. 3-5, 1967	36	32	39	
Totals	49	58	55	.78n.s.

Table 11. Distribution of *Microtus pennsylvanicus* captures by consective periods of the sessions.

	1	2	3	4	5	6	X^2
A. Winter							
Jan.-Mar., 1966	2	-	2	2	-	-	
Jan.-Mar., 1967	3	-	1	4	-	-	
Jan.-Mar., 1968	11	2	1	2	2	2	
Totals	16	2	4	8	2	2	27.41**
B. Snow-free							
Aug. 30-Sept. 1, 1966	6	3	9	4	5	11	
Nov. 3-5, 1966	1	1	1	2	1	-	
Apr. 28-30, 1967	3	2	1	-	1	4	
Aug. 3-5, 1967	19	17	24	17	27	31	
Totals	29	23	26	19	29	35	5.70n.s.

captures. It is obvious that during the winter of 1968 meadow mice were captured most readily during the first period of a session, whether this was 0800-1600 or 1600-2400. In 1966 and 1967 captures were not made in disproportionately large numbers during the first period of the sessions. During these two years the 1600-2400 period is represented in Table 11 by the first (1) and fourth (4) periods and more captures occurred during the fourth period than the first. It appears then that the meadow mice were most active under a snow cover during the 1600-2400 period, and were least active during the 2400-0800 period.

The distribution of captures during the snow-free sessions did not differ significantly from a random distribution whether tallied by period of the day (Table 10) or by periods of the session (Table 11). During the snow-free sessions the meadow mice did not exhibit a diel rhythm.

There is not general agreement in the literature concerning the type of diel rhythm exhibited by _Microtus_. Blair (1940) on the basis of field captures and Seabloom (1965) on the basis of laboratory data considered _M. pennsylvanicus_ to be more active at night. Jackson (1908) and Lo Bue and Darnell (1959) considered the species to be diurnal. Bailey (1926), Johnson (1930) and Hamilton (1937a) all said that _M. pennsylvanicus_ was active at all hours with a tendency toward increased activity just before dusk and just after dawn. In addition to these diel rhythms, short (1-4 hour) activity units have been demonstrated by Graham (1968), Hatfield (1940), and Wiegert (1961). Calhoun (1945) and Wiegert (ibid) suggest that _Microtus_ is a very labile genus with respect to activity patterns and the conflicting literature may be a result of activity patterns varying seasonally, geographically, or meteorlogically. In a detailed study of activity patterns in *M. pennsylvanicus*, Graham (ibid) noted that those animals in field inclosures were more diurnal, those in outside cages were crepuscular, and those in laboratory cages were more nocturnal. He also found that in none of the conditions were all of the voles synchronous.

In the present study diel activity appeared to be equal in all three periods of the day during the snow-free sessions and appeared to be more heavily concentrated in the 1600-2400 period during the winter sessions. Hatfield (1940) said that a 2 to 4 hour rhythm of food getting activity was maintained from 0° to 28° C. no matter what the condition of the lighting, but at 0° the length of each active period was shortened. In the present study the temperature of the subnivean air space was 0° or below. Graham (1968) also said that meadow mice were active a greater percentage of the time in the summer than in the winter. A slight tendency toward greater activity just before dusk and low level of activity could result in the larger number of captures in the 1600-2400 period during the winter. In the summer a slight tendency toward greater activity during part of the day would be marked by a very high overall level of activity, i.e., an animal can only be caught once during any one period.

Clethrionomys gapperi

The distribution of captures of red-backed voles by period of the day during the winter sessions did not differ significantly from a random distribution (Table 12). When the distribution of captures is listed by periods of the session (Table 13) there is no indication that this apparent lack of diel rhythm is not real.

There were only 4 captures of red-backed voles during the snow-free sessions when traps were checked at 8 hour intervals (Tables 12 and 13). The distribution of these 4 captures only indicates that there was no apparent marked diel rhythm.

Under experimental laboratory conditions of constant temperature and humidity Getz (1968a) found activity of red-backed voles during periods of light to be only 30-40% of that during periods of dark. When placed in constant darkness this pattern remained. In another study (Getz, 1968c) temperature and humidity were manipulated but did not change the basic diel pattern. During this study there was no indication of increased diurnal activity when the cages were covered with 20 to 25 cm. of snow. These two laboratory studies are not in agreement with the winter trapping by Pruitt (1959a) of a closely related species (C. rutilus). Pruitt noted an apparent lack of diel rhythm in activity when trapping under a heavy snow cover. Although the numbers are small, the present study also indicates a lack of a diel rhythm under a heavy snow cover.

Peromyscus sp.

There was only one capture of a deer mouse during all the winter sessions and only 6 captures during the 4 snow-free sessions under consideration. All of these captures occurred

Table 12. Distribution of *Clethrionomys gapperi* captures by period of the day.

	2400-0800	0800-1600	1600-2400	X^2
A. Winter				
Jan.-Mar., 1966	-	-	-	
Jan.-Mar., 1967	6	4	5	
Jan.-Mar., 1968	1	2	3	
Totals	7	6	8	.30n.s.
B. Snow-free				
Aug. 30-Sept. 1, 1966	-	-	-	
Nov. 3-5, 1966	-	-	-	
Apr. 28-30, 1967	-	1	1	
Aug. 3-5, 1967	1	-	1	
Totals	1	1	2	.07n.s.

Table 13. Distribution of <u>Clethrionomys gapperi</u> captures by consecutive periods of the sessions.

	1	2	3	4	5	6	X^2
A. Winter							
Jan.-Mar., 1966	-	-	-	-	-	-	
Jan.-Mar., 1967	1	-	2	-	4	2	
Jan.-Mar., 1968	2	-	1	1	1	1	
Totals	3	-	3	1	5	3	3.60n.s.
B. Snow-free							
Aug. 30-Sept. 1, 1966	-	-	-	-	-	-	
Nov. 3-5, 1966	-	-	-	-	-	-	
Apr. 28-30, 1967	-	-	1	1	-	-	
Aug. 3-5, 1967	-	-	-	-	1	1	
Totals	-	-	1	1	1	1	.26n.s.

during the 1600-2400 period (Table 14). The distribution of captures during the snow-free sessions is a significant deviation from a random distribution. The distribution of captures by consecutive periods of the sessions gives no indication that this marked diel rhythm is not real (Table 15). The single winter capture occurred during the seventh period of the trapping session, i.e., the first period of the third day of trapping.

The literature concerning activity patterns in mice of the genus *Peromyscus* is in complete agreement that these mice are strongly nocturnal (c.f. Behney, 1936; Hammer, 1969; Johnson, 1926; Orr, 1959). All of these writers found activity confined almost completely to the dark hours. Johnson (ibid) determined that *P. leucopus* maintained their diel activity pattern even after a month in darkness. He further found that the pattern could be reversed by lighting the experimental room when it was dark outside. Johnson was unable to impose a 16 hour periodicity on the mice, however, and came to the conclusion that the activity rhythm of the mice "...is to be considered an expression of an internal physiological rhythm". The sharply nocturnal distribution of captures in the present study, during the snow-free sessions, is expected therefore.

Orr (1959) suggested the possibility that some daylight activity might occur when light is screened out by a snow cover or when food is scarce. Behney (1936) found that *P. leucopus* kept in outside cages were only active at night except when there was an accumulation of snow or a scarcity of food. This would suggest

Table 14. Distribution of *Peromyscus* sp. captures by period of the day.

	2400-0800	0800-1600	1600-2400	X^2
A. Winter				
(Jan.-Mar.)	-	-	1	.26n.s.
B. Snow-free				
(Apr.-Nov.)	-	-	6	8.37*

Table 15. Distribution of *Peromyscus* sp. captures by consecutive periods of the sessions.

	1	2	3	4	5	6	X^2
A. Winter							
(Jan.-Mar.)	-	-	-	-	-	-	
B. Snow-free							
(Apr.-Nov.)	1	2	-	1	2	-	1.50n.s.

that the very strong nocturnal activity pattern might be modified to some degree under a heavy snow cover. It has already been pointed out however that *Peromyscus* kept in complete darkness maintain a basic nocturnal activity pattern. In a field study in northern Utah, Schmid (1968) found that the nocturnal activity pattern of *P. maniculatus* did not change after a snow cover developed. The single winter capture in the present study does little to shed light on the problem of diel activity under a heavy snow. It has already been suggested (see Distribution) that the single capture indicates that *Peromyscus* are extremely inactive under winter conditions similar to those in the present study.

Blarina brevicauda

The distribution of captures of short-tailed shrews by period of the day is given in Table 16. Neither the winter data nor the snow-free data indicate a diel rhythm. The distribution of captures by periods of the sessions is given in Table 17.

Blair (1941a) said that short-tailed shrews were usually trapped during the night. Martinsen (1969) however, found that *Blarina* maintained in the laboratory had short periods of activity in which activity was continuous, and these periods of activity were spread throughout night and day. The results of the present study tend to support the idea that the short-tailed shrew is arhythmic with respect to a diel activity pattern.

Table 16. Distribution of *Blarina brevicauda* captures by period of the day.

	2400-0800	0800-1600	1600-2400	X^2
A. Winter				
Jan.-Mar., 1966	1	-	-	
Jan.-Mar., 1967	10	20	17	
Jan.-Mar., 1968	1	1	1	
Totals	12	21	18	2.47n.s.
B. Snow-free				
Aug. 30-Sept. 1, 1966	1	2	2	
Nov. 3-5, 1966	1	1	-	
Apr. 28-30, 1967	-	-	-	
Aug. 3-5, 1967	-	-	1	
Totals	2	3	3	.03n.s.

Table 17. Distribution of *Blarina brevicauda* captures by consecutive periods of the sessions.

	1	2	3	4	5	6	X^2
A. Winter							
Jan.-Mar., 1966	-	1	-	-	-	-	
Jan.-Mar., 1967	4	2	5	6	7	10	
Jan.-Mar., 1968	1	-	-	-	1	1	
Totals	5	3	5	6	8	11	7.59n.s.
B. Snow-free							
Aug. 30-Sept. 1, 1966	2	-	-	-	1	2	
Nov. 3-5, 1966	-	-	1	-	1	-	
Apr. 28-30, 1967	-	-	-	-	-	-	
Aug. 3-5, 1967	-	-	-	-	1	-	
Totals	2	-	1	-	3	2	2.24n.s.

ANALYSIS OF THE STUDY TECHNIQUE

The technique of using chimneys to trap small mammals in the subnivean space worked very well. The technique not only made winter trapping practical but also served to protect the live traps in summer. The live traps were left in the chimneys during the entire study. The traps could be left in the study area saving time and effort every time a new session was started. The animals in the area quickly accepted the chimneys as part of the environment - nests were often found in the chimneys at the start of a new session.

Pruitt (1959a) said that approximately 60 cm. of light taiga snow was necessary before venturing onto the study area. In the present study, however, trapping was carried out several times in the winter with a snow depth of only 15-20 cm. I was extremely careful to place my snowshoe in the same spot on the back side of the chimney every time. I feel that by using this technique only a small area of the subnivean space next to the chimney was destroyed. In areas with a light snow cover snowshoes would not need to be used at all. A boot will destroy less subnivean air space, after all, than a snowshoe. In my opinion the primary purpose of the snowshoe is not to protect the subnivean air space but to aid in locomotion.

The chimney technique could be used to great advantage in any long term study, with one notable exception. The chimneys could probably not be used in areas exposed to strong winds. Wind forms a hollow in the snow around each chimney. In strong winds this hollow would undoubtedly reach the ground and the chimneys would be in isolated pockets with no snow cover.

In the present study a hollow started forming around each chimney in early March due to the effect of radiation on the chimneys. These hollows began reaching ground level by mid-March. The chimneys might be of limited usefulness between this time and the disappearance of most of the rest of the snow. In the present study it was not possible to trap during this period and this limitation could not be tested.

Pruitt (personal communication) said that checking the traps at least every 10 hours and sufficient bait in the traps were more important than nesting material for survival of small mammals in cold weather. He felt, in fact, that nesting material was useless because the urine froze in the bedding. In the present study animals were lost during the first session of the first winter when the traps were left set over night, approximately 16 hours. Animals were also lost to the cold in the period of time between picking up the trap and the examination of the animal. After modifying the technique so as to check the traps at 8 hour intervals and by transporting the animals in a styrofoam chest, very few animals were lost. After adopting the above modifications in technique, there were only two deaths, one *M. pennsylvanicus* and one *B. brevicauda*, out of a total of 110 winter captures of the four species considered in this study.

A small canvas ice house used in this study proved to be invaluable. During the entire study it served as a storage area for spare traps, weighing and measuring apparatus, and other tools.

In the winter the shelter was absolutely necessary for the examination of the animals. It was very comfortable in the still air of the ice house and a Coleman lantern provided enough heat to keep the hands warm and supple. It is impossible, with stiff cold hands, to examine and make linear measurements on small, live mammals.

SUMMARY

1. Very little is known concerning the winter ecology of the small winter-active mammals in regions with a persistent snow cover.
2. The purpose of this study was basically three-fold. First, to determine if there are seasonal changes in distribution of small winter-active mammals across a sharp wood-meadow transition; second, to gather field growth data on these animals; and third, to evaluate and develop a winter live-trapping technique.
3. The study area consisted of an old field, uncultivated since 1928, and adjacent stands of planted jack pine, planted red pine, young aspen, and mature aspen. The transitions between all areas were very sharp.
4. Live-traps were set in a grid pattern with 35 feet between traps. The traps were maintained in wooden chimneys, which made it possible to trap below the snow cover in the winter without disturbing the snow cover. Distribution and weight and measurement records were maintained for all winter-active mammals trapped.
5. Meadow mice (<u>Microtus pennsylvanicus</u>) were found in the meadow, young aspen, and red pine in the snow-free months, but were most heavily concentrated in the meadow. In the winter meadow mice were found only in the meadow and primarily in the part of the meadow where brome grass (<u>Bromus inermis</u>) is dominant. There was no indication of individual movement

between seasons.

6. Red-backed voles (Clethrionomys gapperi) were found only in the mature and young aspen habitats during both winter and snow-free seasons. This specie was equally distributed between these habitats during the winter but was more concentrated in the mature aspen during the snow-free season. There was no indication of individual movement between seasons.
7. Deer mice (Peromyscus sp.) were concentrated in the mature aspen during the snow-free season and were never captured in the meadow during this season. There was only one winter capture of a deer mouse.
8. Short-tailed shrews (Blarina brevicauda) were distributed equally across all habitats during the snow-free season and were distributed equally across all but the Poa-Phleum-Carex portion of the meadow during the winter. This area was avoided by otherwise widely ranging individual shrews.
9. Interactions between meadow mice and red-backed voles may have partially restricted the habitats of both.
10. Short-tailed shrews apparently had little effect on the distribution of meadow mice.
11. The winter avoidance of the Poa-Phleum-Carex portion of the meadow by both Microtus and Blarina may be because of a less well developed subnivean air space.
12. A measurement of the reliability of weights and linear measurements made on living small mammals is given for the first time and indicates that linear measurements are a great

deal more reliable than weight measurements.

13. *M. pennsylvanicus* born by early May reached their maximum size by late July. These animals undergo a sharp loss in weight starting in early August.

14. *M. pennsylvanicus* born after early or mid-May experience a seasonal stoppage of growth by late August to mid-September. There is then no growth until sometime between mid-March and early April.

15. The short-tailed shrews (*B. brevicauda*) captured in the winter were as large and as heavy as the summer animals. The evidence indicated that there was no weight loss in the fall.

16. Activity of meadow mice (*M. pennsylvanicus*) appeared to be equal in all three periods of the day during the snow-free sessions but was more heavily concentrated in the 1600-2400 period during the winter sessions.

17. Activity of red-backed voles (*C. gapperi*) appeared to be equal in all three periods of the day during the winter sessions.

18. All activity of deer mice (*Peromyscus* sp.) appeared to be restricted to the 1600-2400 period during the snow-free season. The one winter capture also occurred during the 1600-2400 period.

19. Short-tailed shrews (*B. brevicauda*)were arhythmic with respect to a diel activity pattern during both the winter and snow-free seasons.

20. The chimney technique originally used for winter live-trapping of small mammals in the Alaskan taiga was easily adapted to a live-trapping study in northern Minnesota.

REFERENCES CITED

Ackerfors, H. G. E. 1964. Vinteraktiva nabbmoss under snon. (Winter active shrews in the subnivean environment) Zool. Revy, 26:16-22.

Bader, H. et al. 1954. Snow and its metamorphosis. SIPRE Translation No. 14 of Bader, H., R. Haefli, E. Bucher, J. Neher, O. Eckel and Chr. Thams-1939-Der Schnee und seine Metamorphose. Beiträge zur Geologie der Schweiz. Geotechnische Serie, Hydrologie, Zieferung 3, Bern.

Bailey, V. 1926. Mammals of North Dakota. North Amer. Fauna, No. 49, 226 pp.

Barbehenn, K. R. 1955. A field study of growth in Microtus pennsylvanicus. Jour. Mammal, 36:533-543.

_____. 1958. Spacial and population relationships between Microtus and Blarina. Ecology, 39:293-304.

Beckwith, S. L. 1954. Ecological succession on abandoned farm lands and its relationship to wildlife management. Ecol. Monogr., 24:349-375.

Bee, J. W. and E. R. Hall. 1956. Mammals of northern Alaska on the arctic slope. Univ. Kan. Mus. Nat. Hist. Misc. Publ. No. 8:1-309.

Beer, J. R. 1961. Winter home ranges of the red-backed mouse and the white-footed mouse. Jour. Mammal., 42:174-180.

_____. 1964. Bait preferences of some small mammals. Jour. Mammal., 45:632-634.

Behney, W. H. 1936. Nocturnal explorations of the forest deermouse. Jour. Mammal., 17:225-230.

Bergstedt, B. 1965. Distribution, reproduction, growth and dynamics of the rodent species Clethrionomys glareolus (Schreber), Apodemus flavicollis (Melchior) and Apodemus sylvaticus (Linne) in southern Sweden. Oikos, 16:132-160.

Blair, W. E. 1940. Home ranges and populations of the meadow vole in southern Michigan. Jour. Wild. Mgmt., 4:149-161.

_____. 1941a. Some data on the home ranges and general life history of the short-tailed shrew, red-backed vole, and woodland jumping mouse in northern Michigan. Am. Midl. Nat., 25:681-685.

Blair, W. E. 1941b. Techniques for the study of mammal populations. Jour. Mammal., 22:148-157.

Buell, M. F. and J. E. Cantlon. 1950. A study of two communities of the New Nersey pine barrens and a comparison of methods. Ecology, 31:567-586.

_____. and W. E. Gordon. 1945. Hardwood-conifer forest contact in Itasca Park, Minnesota. Am. Midl. Nat., 34:433-439.

Burt. W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Mich., 45:1-58.

Butsch, R. S. 1954. The life history and ecology of the red-backed vole, Clethrionomys gapperi gapperi Vigors, in Minnesota. Unpublished Ph.D. Thesis, Univ. of Mich. 148 pp.

Calhoun, J. B. 1945. Diel activity rhythms of the rodents Microtus ochrogaster and Sigmodon hispidus hispidus. Ecology, 26:251-273.

_____. 1963. The social use of space. pp. 1-187. In Physiological Mammology Vol. 1 (Mayer, W. V. and R. G. Van Gelder, eds.), Academic Press, New York, 381 pp.

Cameron, A. W. 1964. Competitive exclusion between the rodent genera Microtus and Clethrionomys. Evolution, 18:630-634.

Chenoweth, H. 1917. The reactions of certain moist forest mammals to air conditions and its bearing on problems of mammalian distribution. Biol. Bull., 32:183-201.

Chew, R. M. and B. B. Butterworth. 1959. Growth and development of Merriam's kangaroo rat, Dipodomys merriami. Growth, 23:75-95.

Chitty, D. 1952. Mortality among vole (Microtus agrestis) at Lake Vyronwy, Montgomeryshire in 1936-9. Phil. Trans. Roy. Soc. London, Series B, 236:505-552.

Clough, G. C. 1964. Local distribution of two voles: evidence for interspecific interation. Can. Field-Nat., 78:80-89.

Cook, E. F. and J. R. Beer. 1958. A study of louse populations on the meadow vole and deer mouse. Ecology, 39:645-659.

Cottam, G. and J. F. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology, 37:451-460.

Coulianos, C. C. and A. G. Johnels. 1962. Note on the subnivean environment of small mammals. Arkiv For Zoologi, 15:363-370.

Curtis, J. and R. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology, 32:476-496.

Dapson, R. W. 1968. Growth patterns in a post-juvenile population of short-tailed shrews (Blarina brevicauda). Amer. Midl. Nat., 79:118-129.

Dawson, N. J. 1967. The surface-area, body-weight relationship in mice. Aus. Jour. Biol. Sci., 20:687-690.

Dehnel, A. 1949. Studies on the genus Sorex L. Ann. Univ. M. Curie-Sktodowska. Sect. C, 4:17-97. (In Polish with English summary).

Dobie, J. 1959. The Itasca Story. Ross and Haines, Minneapolis, 202 pp.

Eadie, W. R. 1944. The short-tailed shrew and field mouse predation. Jour. Mammal., 25:359-365.

_____. 1948. Shrew-mouse predation during low mouse abundance. Jour. Mammal., 29:35-37.

_____. 1952. Shrew predation and vole populations on a localized area. Jour. Mammal., 33:185-189.

_____. 1953. Response of Microtus to vegetative cover. Jour. Mammal., 34:263-264.

Elsner, R. W. and W. O. Pruitt, Jr. 1959. Some structural and thermal characteristics of snow shelters. Arctic, 12:20-27.

Findley, J. S. 1954. Competition as a possible limiting factor in the distribution of Microtus. Ecology, 35:418-420.

Formozov, A. N. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Occas. Publ. No. 1, Boreal Institute, Univ. of Alberts (Original in Russian in: Materials for Fauna and Flora of USSR. New Series, Zoology, 5:1-152 Moscow Society of Naturalists).

a

Frenzel, L. D. 1957. A study of small-mammal populations of State Island, Basswood Lake, Minnesota. Unpublished Ph.D. Thesis, Univ. of Minn., 232 pp.

Fuller, W. A., L. L. Stebbins and G. R. Dyke. 1969. Overwintering of small mammals near Great Slave Lake, northern Canada. Arctic, 22:34-55.

Getz, L. L. 1961a. Factors influencing the local distribution of _Microtus_ and _Synaptomys_ in Southern Michigan Ecology, 42:110-119.

_____. 1961b. Factors influencing the local distribution of shrews. Amer. Midl. Nat., 65:67-88.

_____. 1961c. Home ranges, territoriality, and movement of the meadow vole. Jour. Mammal., 42:24-36.

_____. 1961d. Notes on the local distribution of _Peromyscus leucopus_ and _Zapus hudsonias_. Amer. Midl. Nat., 65:486-500.

_____. 1962. Aggressive behavior of the meadow and prairie voles. Jour. Mammal., 43:351-358.

_____. 1968a. Influence of light on the activity of the red-backed vole. Univ. Connecticut Occas. Papers, Biol. Sci. Ser., 1:83-107.

_____. 1968b. Influence of water balance and microclimate on the local distribution of the red-back vole and white-footed mouse. Ecology, 49:276-286.

_____. 1968c. Influence of weather on the activity of the red-backed vole. Jour. Mammal., 49:565-570.

Gleason, H. A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand, Princeton, 810 pp.

Golley, F. G. 1961. Interaction of natality, mortality and movement during an annual cycle in a _Microtus_ population. Amer. Midl. Nat., 66:152-159.

Gottschang, J. L. 1965. Winter populations of small mammals in old fields of southwestern Ohio. Jour. Mammal., 46:44-52.

Graham, W. J. 1968. Daily activity patterns in the meadow vole, _Microtus pennsylvanicus_. Dissertation Abs. B, 29:1211.

Gunderson, H. L. 1950. A study of some small mammal populations at Cedar Creek Forest, Anoka County, Minnesota. Occ. Pap. Minn. Mus. Nat. Hist., No. 4:1-49.

_____. 1959. Red-backed vole habitat studies in central Minnesota. Jour. Mammal., 40:405-412.

_____. 1953. The mammals of Minnesota. Univ. of Minn. Press, Minneapolis, 190 pp.

Hamilton, W. J., Jr. 1937a. Activity and home range of the field mouse, Microtus pennsylvanicus pennsylvanicus (Ord). Ecology, 18:255-263.

_____. 1937b. Growth and life span of the field mouse. Amer. Naturalist, 71:500-507.

_____. 1941. Reproduction of the field moust Microtus pennsylvanicus (Ord). Cornell Univ. Exp. Sta. Mem., 237:1-23.

Hammer, D. A. 1969. Changes in the activity patterns of deer mice (Peromyscus maniculatus) caused by wind. Jour. Mammal., 50:811-815.

Harrington, E. J. 1955. A study of postnatal skeletal development and age determination in the meadow-mouse, Microtus pennsylvanicus (Ord). Dissertation Aba. B. 15:2606.

Hatfield, D. 1940. Activity and food consumption in Microtus and Peromyscus. Jour. Mammal., 21:29-36.

Hnatiuk, J. and S. Iverson. 1965. Habitat distribution and morphological variation of the deer mouse (Peromyscus) complex in north-western Minnesota and north-eastern North Dakota. Proc. North Dakota Acad. Sci., 19:147-148.

Hoffmeister, D. F. and L. L. Getz. 1968. Growth and age-classes in the prairie vole, Microtus ochrogaster. Growth, 32:57-69.

Howard, W. E. 1951. Relation between low temperature and available food to survival of small rodents. Jour. Mammal., 32:300-312.

Iverson, S. L., R. W. Seabloom and J. M. Hnatiuk. 1967. Small-mammal distributions across the prairie-forest transition of Minnesota and North Dakota. Amer. Midl. Nat., 78:188-197.

Jackson, H. G. 1908. A preliminary list of Wisconsin mammals. Bull. Wis. Nat. Hist. Soc., 6:13-35.

Jameson, E. W., Jr. 1949. Some factors influencing the local distribution and abundance of woodland small mammals in central New York. Jour. Mammal., 30:221-235.

Johnson, H. M. 1954. Winter microclimates of importance to Alaskan small mammals and birds. Unpublished Ph.D. Thesis, Cornell Univ., 109 pp.

Johnson, M. S. 1926. Activity and distribution of certain wild mice in relation to biotic communities. Jour. Mammal., 7:245-277.

Johnson, M. S. 1930. Common injurious mammals of Minnesota. Univ. Minn. Agric. Exper. Stat. Bull., 259:1-67.

Koplin, J. R. and R. S. Hoffmann. 1968. Habitat overlap and competitive exclusion in voles (Microtus). Amer. Midl. Nat., 80:494-507.

Lewin, D. C. 1968. Notes on the habitat of Microtus in central Illinois. Ecology, 49:791-792.

LoBue, J. and R. M. Darnell. 1959. Effect of habitat disturbance on a small mammal population. Jour. Mammal., 40:425-437.

MacKay, A. A. 1962. An easy method of trapping small taiga mammals in winter. Jour. Mammal., 43:556-557.

Manville, R. H. 1949. A study of small mammal populations in northern Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 73:1-83.

Morhardt, J. E. and J. W. Hudson. 1966. Daily torpor induced in white-footed mice (Peromyscus spp.) by starvation. Nature, 212:1046-1047.

Morris, R. D. 1969. Competitive exclusion between Microtus and Clethrionomys in the aspen parkland of Saskatchewan. Ecology, 50:291-301.

Nicholson, A. J. 1941. The homes and social habits of the wood-mouse (Peromyscus leucopus noveboracensis) in Southern Michigan. Amer. Midl. Nat., 25:196-223.

Odum, E. P. 1944. Water consumption of certain mice in relation to habitat selection. Jour. Mammal., 25:404-405.

Orr, H. D. 1959. Activity of white-footed mice in relation to environment. Jour. Mammal., 40:213-221.

Pearson, O. P. 1945. Longevity of the short-tailed shrew. Amer. Midl. Nat., 34:531-546.

Plummer, J. T. 1844. Scraps in natural history (Quadrupeds). Amer. Jour. Sci. Arts, 46:236-249.

Pruitt, W. O., Jr. 1953. An analysis of some physical factors affecting the local distribution of the short-tail shrew (Blarina brevicauda) in the northern part of the lower peninsula of Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 79:1-39.

_____. 1957. Observations on the bioclimate of some taiga mammals. Arctic, 10:131-138.

Pruitt, W. O., Jr. 1959a. A method of live-trapping small taiga mammals in winter. Jour. Mammal., 40:139-143.

______. 1959b. Microclimates and local distribution of small mammals on the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 109:1-27.

______. 1960. Animals in the snow. Sci. Amer., 202:60-68.

Pucek, Z. 1964. August Dehnel, his life and work. Acta Theriologica, 8:1-10.

Schmid, G. G. 1968. An ecological study of several small mammals in northern Utah. Master of Science Education Thesis, Univ. of Utah, 64 pp.

Scholander, P. G., Hock, R., Walters, V. and L. Irving. 1950a. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull., 99:259-271.

______. Hock, R., Walters, V., Johnson, F., and L. Irving. 1950b. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull., 99:237-258.

______. Walters, V., Hock, R., and L. Irving, 1950c. Body insulation of some arctic and tropical mammals and birds. Biol. Bull., 99:225-236.

Schwarz, S. S., A. V. Pokrovski, V. G. Istchenko, V. G. Olenjev, N. A. Ovtschinnikova, and O. A. Piastolova. 1964. Biological peculiarities of seasonal generations of rodent, with special reference to the problem of senescence in mammals. Acta Theriologica, 8:11-43.

Seabloom, R. W. 1965. Daily motor activity and corticosterone secretion in the meadow vole. Jour. Mammal., 46:286-295.

Sealander, J. A. 1966. Seasonal variations in hemoglobin and hematocrit values in the northern red-backed mouse, Clethrionomys rutilus dawsoni (Marriam), in interior Alaska. Can. Jour. Zool., 44:213-224.

Sheppe, W. 1967. Habitat restriction by competitive exclusion in the mice Peromyscus and Mus. Can. Field Nat., 81:81-98.

Spurr, S. H. 1954. The forests of Itasca in the nineteenth century as related to fire. Ecology, 35:21-25.

Stebbins, L. L. 1968. Seasonal and latitudinal variations in the circadian rhythms of three species of small rodents in northern Canada. Ph.D. Thesis, University of Alberta, Edmonton, 68 pp.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill, New York, 481 pp.

Thompson, D. Q. 1965. Food preferences of the meadow vole (Microtus pennsylvanicus) in relation to habitat affinities. Amer. Midl. Nat., 75:76-86.

Thomsen, H. P. 1945. The winter habits of the northern white-footed mouse. Jour. Mammal., 26:138-142.

U. S. Dept. of Commerce Weather Bureau Climatological Data, Annual Summaries, 1931-1968.

Van Vleck, D. B. 1968. Movements of Microtus pennsylvanicus in relation to depopulated areas. Jour. Mammal., 49:92-103.

Weese, A. O. 1924. Animal ecology of an Illinois elm-maple forest. Illinois Biol. Monogr., 9: No. 4.

Whitmoyer, T. F. 1956. A laboratory study of growth rate in young Microtus pennsylvanicus. Master of Science Thesis, Michigan State University, 62 pp.

Wiegert, R. G. 1961. Respiratory energy loss and activity patterns in the meadow vole, Microtus pennsylvanicus. Ecology, 42:245-253.

Wirtz, W. O., II, and P. G. Pearson. 1960. A preliminary analysis of habitat orientation in Microtus and Peromyscus. Am. Midl. Nat. 63:131-142.

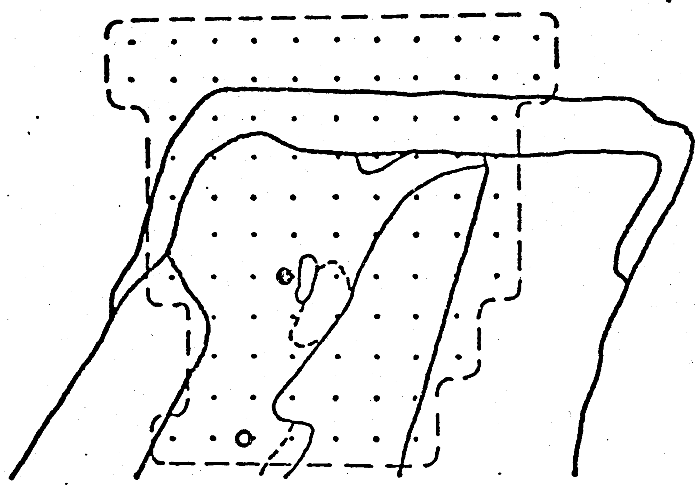
Wood, F. E. 1910. Mammals of Champaign County. Bull. Illinois State Lab. Nat. Hist., 8:501-613.

Zimmerman, E. G. 1965. A comparison of habitat and food of two species of Microtus. Jour. Mammal., 46:605-612.

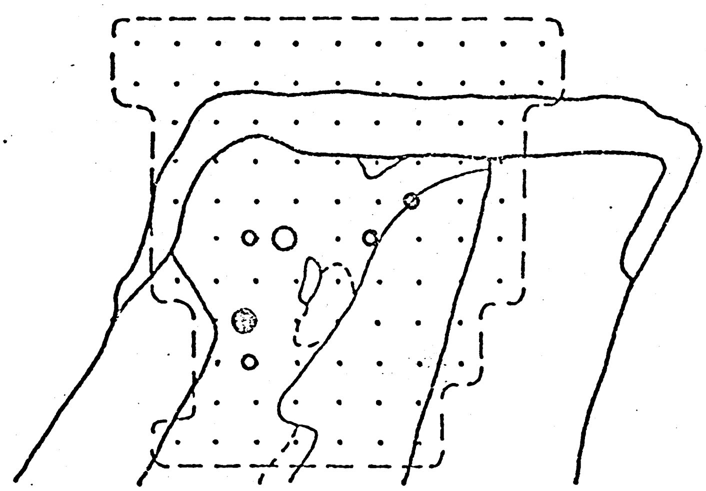
APPENDIX A

Microtus pennsylvanicus captured during both winter and summer.

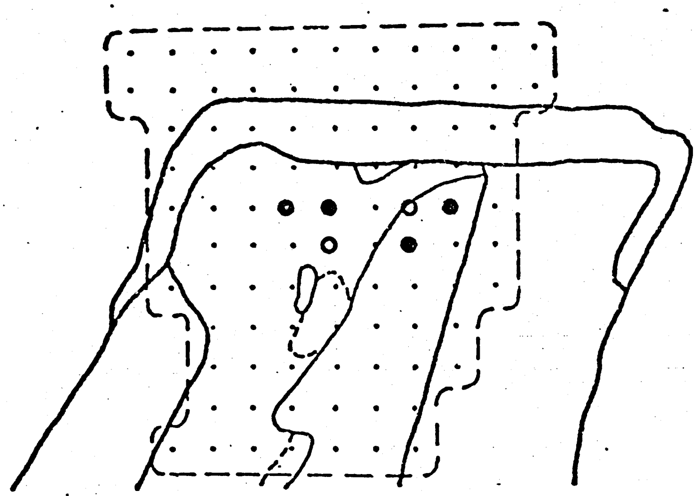
Summer		Winter
○	1 capture	●
○	2 captures	●
○	3 captures	●
	4 or more captures indicated by numeral in circle	



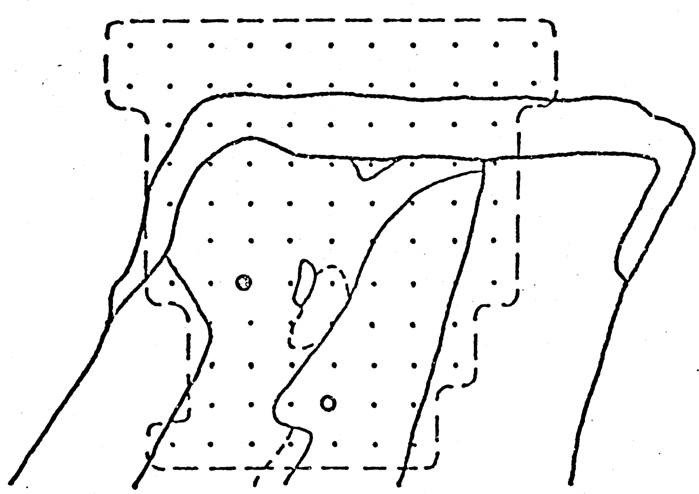
M. pennsylvanicus No. 67 (female).



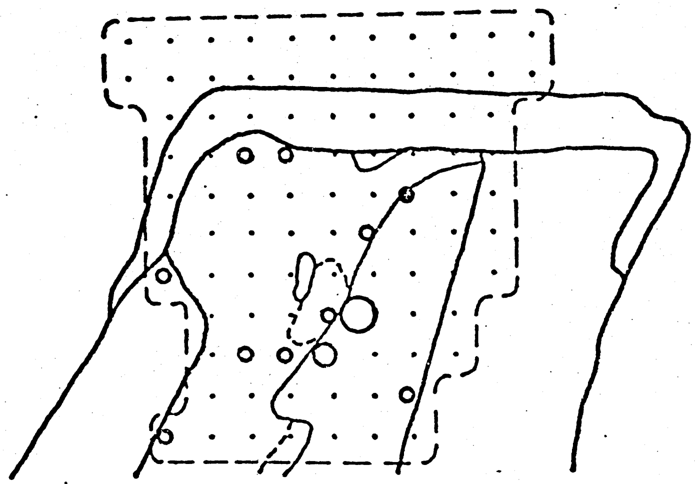
M. pennsylvanicus No. 76 (female).



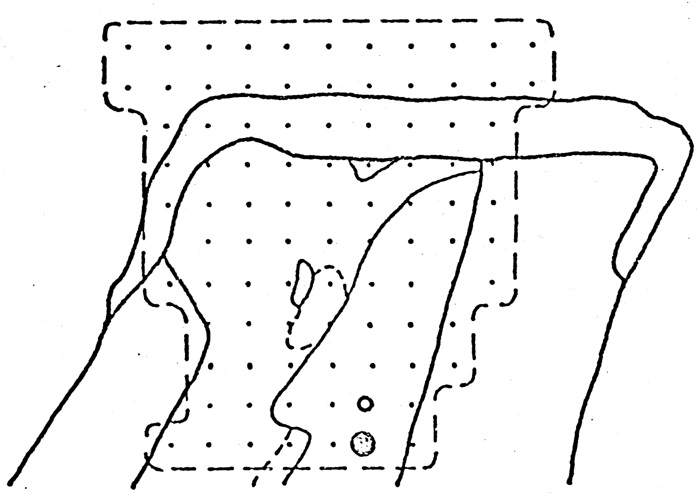
M. pennsylvanicus No. 84 (female).



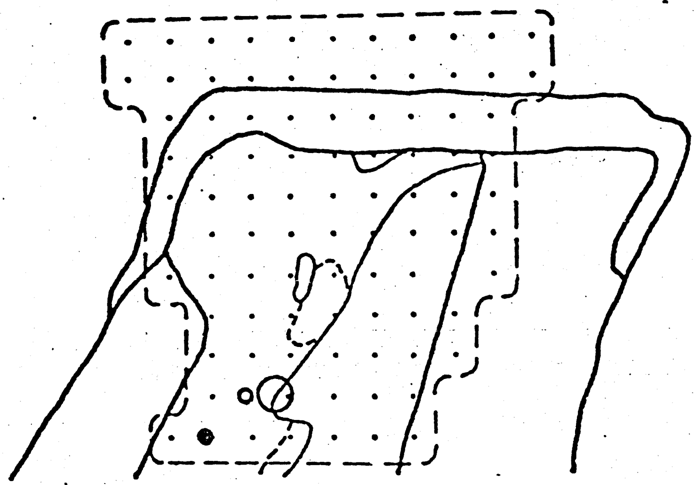
M. pennsylvanicus No. 103 (male).



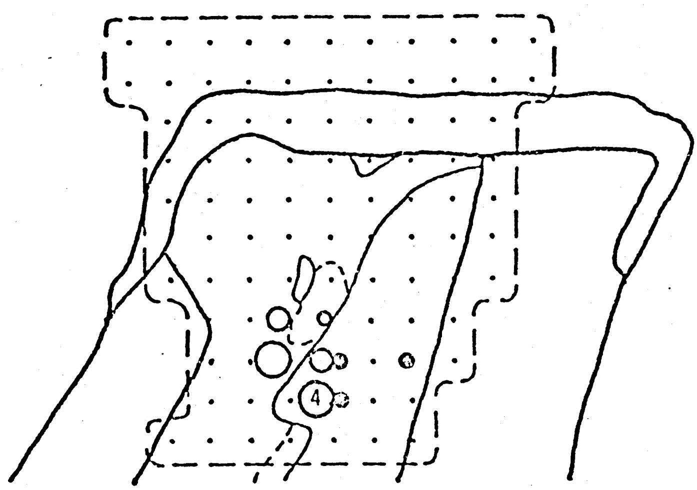
M. pennsylvanicus No. 151 (male).



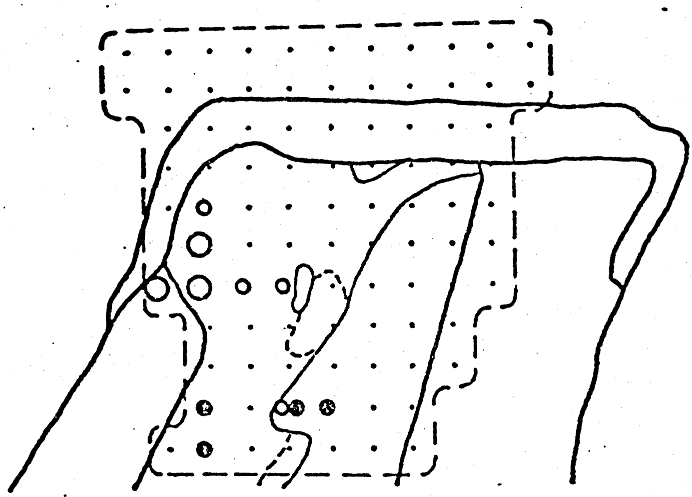
M. pennsylvanicus No. 155 (male).



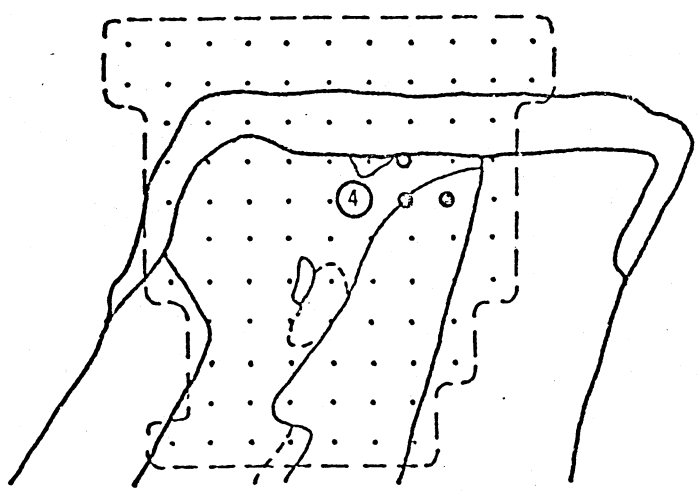
M. pennsylvanicus No. 160 (female).



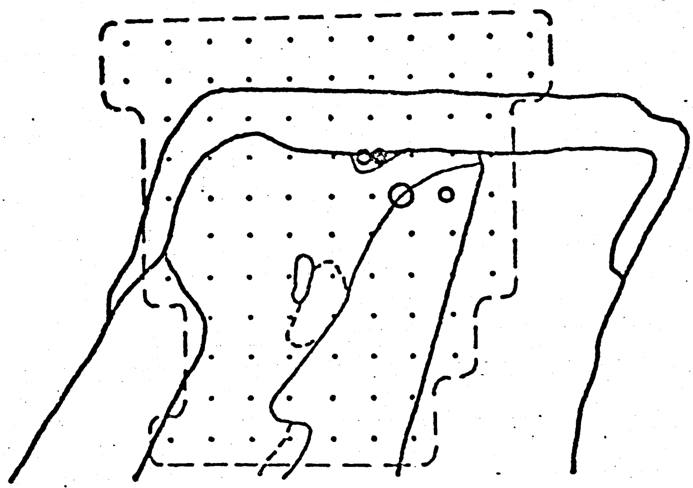
M. pennsylvanicus No. 172 (female).



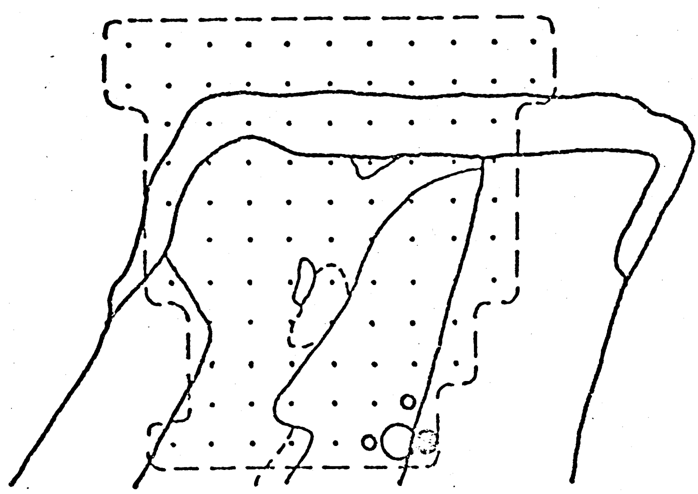
M. pennsylvanicus No. 189 (female).



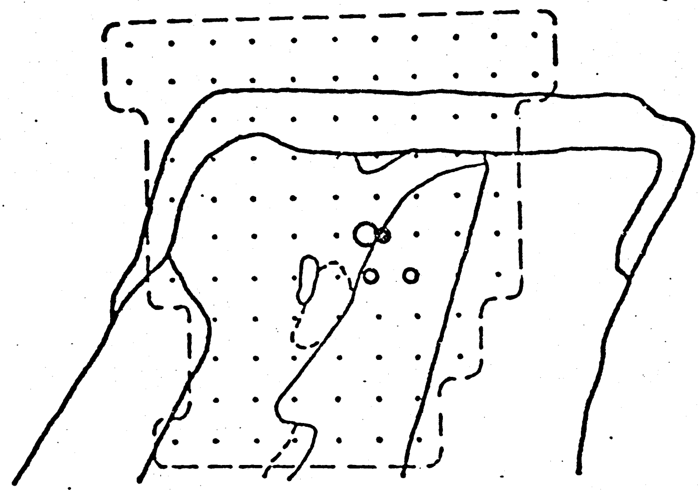
M. pennsylvanicus No. 207 (female).



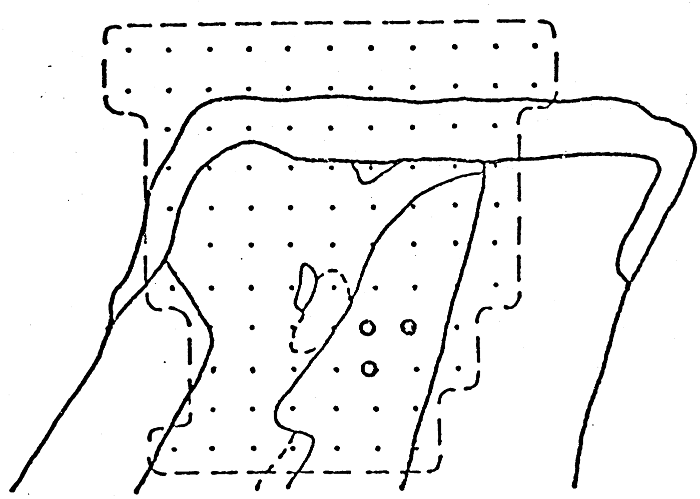
M. pennsylvanicus No. 246 (female).



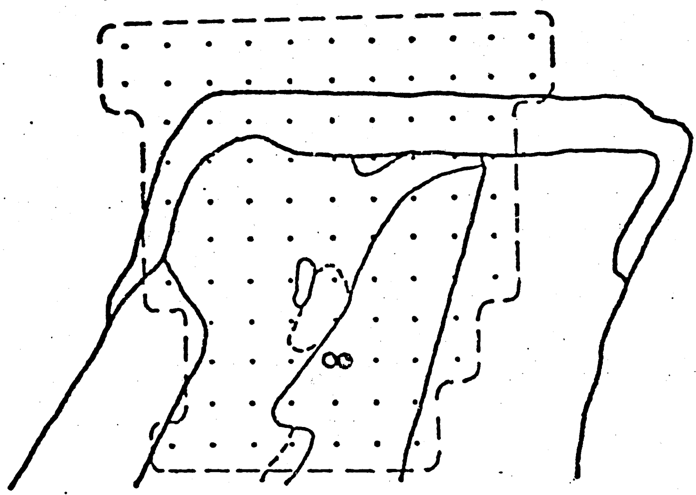
M. pennsylvanicus No. 250 (female).



M. pennsylvanicus No. 252 (male).



M. pennsylvanicus No. 258 (female).

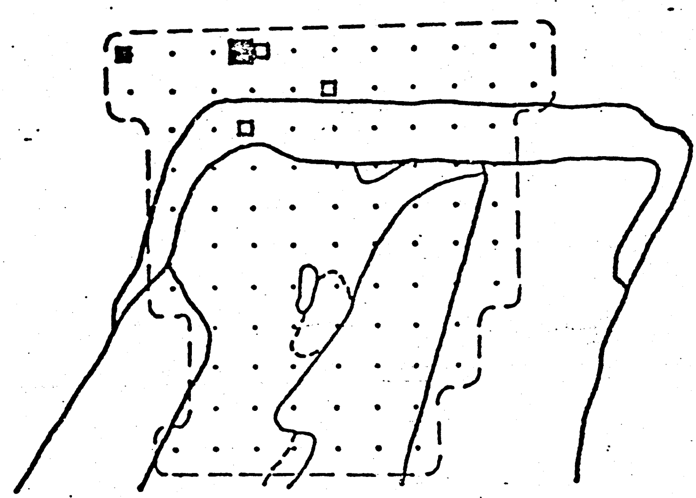


M. pennsylvanicus No. 262 (male).

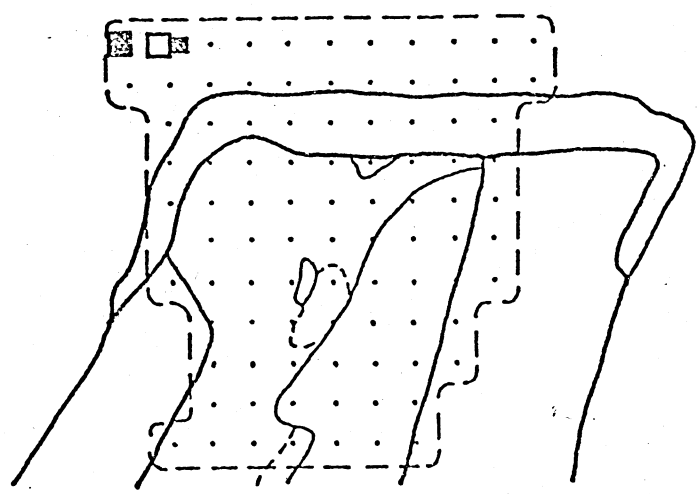
APPENDIX B

Clethrionomys gapperi captured during both winter and summer.

Summer		Winter
▫	1 capture	▪
□	2 captures	■



C. gapperi No. 25 (female).



C. gapperi No. 12 (female).

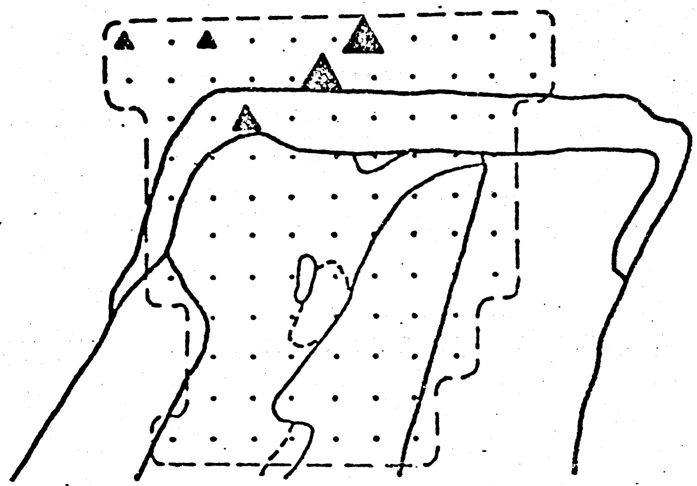
APPENDIX C

Blarina brevicauda captured a number of times during the winter months.

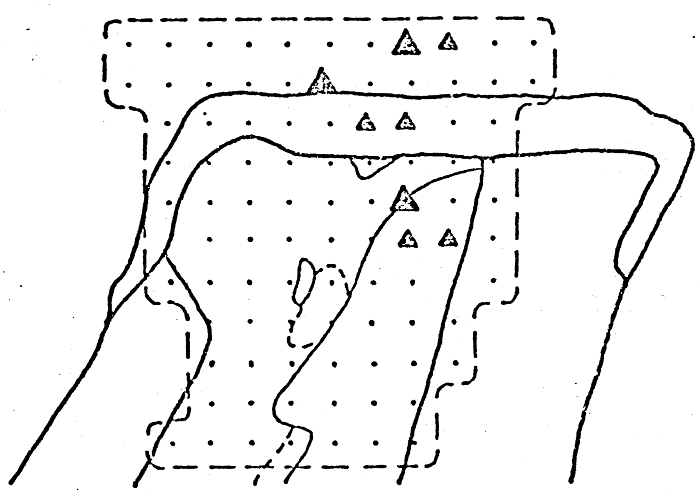
1 capture

2 captures

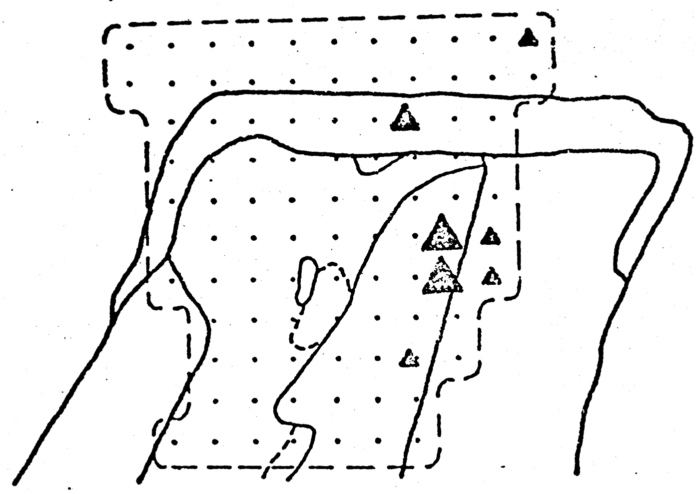
3 captures



B. brevicauda No. 24.



B. brevicauda No. 27.



B. brevicauda No. 30.

Appendix D

Alphabetical listing of all
plant species seen on the study area.

Acer saccharum Marsh.

Achillea millefolium L.

Agropyron repens (L.) Beauv.

Amelanchier sp. Medic.

Anemone canadensis L.

Apocynum androsaemifolium L.

Aster ciliolatus Lindl.

Aster macrophyllus L.

Athyrium filix-femina (L.) Roth.

Bromus inermis Leyss.

Carex atherodes Spreng.

Carex pensylvanica Lam.

Carex rosea Schk.

Cirsium arvense (L.) Scop.

Cirsium vulgare (Savi) Tenore.

Cornus stolonifera Michx.

Corylus americana Walt.

Corylus cornuta Marsh.

Crataegus sp. L.

Festuca rubra L.

Galium boreale L.

Liastris aspera Michx.

Maianthemum canadense Desf.

Muhlenbergia glomerata (Willd.) Trin.

Phleum pratense L.

Pinus bankiana Lamb.

Pinus resinosa Ait.

Pinus strobus L.

Poa palustris L.

Poa pratensis L.

Populus balsamifera L.

Populus tremuloides Michx.

Prunus nigra Ait.

Prunus pennsylvanica L.f.

Prunus serotina Ehrh.

Prunus virginiana L.

Quercus borealis Michx. f.

Quercus macrocarpa Michx.

Rhus radicans L.

Rosa sp. L.

Rubus idaeus L.

Salix sp. L.

Scirpus cyperinus (L.) Kunth.

Solidago canadensis L.

Spirea alba DuRoi.

Stachys palustris L.

Thalictrum dasycarpum Fisch. & Avé-Lall.

Thalictrum dioicum L.

Trifolium hybridum L.

Trifolium pratense L.

Typha lalifolia L.

Ulmus americana L.

Viburnum rafinesquianum Schult.

Vicia americana Muhl.